The influence of *Eucalyptus globulus* Labill. on the environment and vascular plants in a Tasmanian grassy woodland

by

Johny S. Tasirin, Ir., MScF.

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Declaration

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due acknowledgement is made in the text of the thesis.

Johny S. Tasirin

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Abstract

The aims of this thesis are to document and explain heterogeneity creating processes associated with the presence of *Eucalyptus globulus* in a fire-prone grassy woodland ecosystem, with the research hypotheses being that: (1) *Eucalyptus globulus* creates environmental heterogeneity; (2) this induced environmental heterogeneity is reflected in the species richness of the woodland.

Log shadows, linear bare patches, assumed to be the location of burnt fallen logs of *Eucalyptus globulus,* seemed best explained by soil moisture. In comparison to adjacent ground with dense grass cover, the log shadows had: low microbial activity, low N, low SOM, more sand, less silt, less clay and higher infiltration rates. Log shadows parallel to the contours had different patterns to those orthogonal to the contours.

Tree diameter influences floristic composition close to the tree. For plots located immediate to the tree, ordination scores were strongly separated by tree diameter class. The separation became less obvious when the plots were further from the tree base.

Soil available phosphorus and nitrogen did not vary by position in relation to the tree. Organic matter content and particle size in the soils near the tree base is affected by tree size. The highest organic matter and sand contents are found next to the small trees. Soils on the up side of the trunk were more level than

soils on other sides. Rock cover was higher in the down side of the trunk than the up side. Rock cover significantly increased with tree size

The accumulated leaf litterfall under the canopy and in the open was not significantly different by the end of the year. The annual bud and flower litterfall under the canopy of *Eucalyptus globulus* was significantly higher than in the open. Annual fruit litterfall was also significantly greater under the canopy. Significant differences in bark litterfall between under the canopy and the open occur only in November, December and March. Branch litterfall under the canopy was higher than in the open with exception of March. Annual litterfall of possum droppings was also significantly greater under trees.

The majority of nutrients originated from the leaf litter, although most of litter mass comes from bark. Wildlife may be an important component in the cycle of nutrients in the *Eucalyptus globulus* dominated woodlands. In addition to the rapid decay of possum dropping, the average monthly nutrient contents in possum droppings were remarkably higher than other litter materials.

Most of the litterfall occurred under the canopy. If the same amount of litterfall occurred in the open, the release of nutrients from the litter into the system might become much greater since the rates of decomposition of all types of litter were lower under the canopy. These slow rates might relate to low soil moisture content under the canopy.

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Figures

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CHAPTER 1

General Introduction

Plant species richness has been argued to be function of disturbance (Grime, 1979), productivity (Connell, 1978) and relative extinction and speciation rates over geological time. However, it has long been recognized that some plant species, in themselves, can either increase or decrease species richness, by inducing or reducing environmental heterogeneity.

Trees, often dominant in both the structural and ecological sense, provide many excellent examples of this phenomenon. Some, such as many conifers, tend to reduce diversity by forming closed monospecific stands at maturity (Dye *et al.*, 1995). Other monodominants appear to increase opportunities for other species. For example, Gilfedder and Kirkpatrick (1998) and Lunt (1997a, 1997b) suggested that the higher species richness found in *Eucalyptus* grassy woodlands than in grasslands is likely to be attributable to the variations in environment caused by the presence or absence of tree roots and canopies.

Trees may provide substrate or food for vascular and non-vascular plants that may or may not be beneficial to the tree themselves or other plants. Symbiotic relationships are common between eucalypts and various types of mycorrhizal fungi (May and Simpson, 1997). The decayed wood of fallen trees provides

regeneration niches, for example, in Tasmanian mixed forests (McKenny and Kirkpatrick, 1999). Trees are also important for diet and shelter for many animals that, to a degree, can create heterogeneity themselves (Woinarski *et al.*, 1997). Among them, the arboreal folivores that prefer young leaves, such as the possum (*Pseudocheirus peregrinus*), may be important in nutrient cycling (Landsberg and Cork, 1997).

Geomorphologic alteration of soil micro-landscapes caused by root mounding and fallen trees can create gaps that are suitable for disturbance colonizers (Lavorel and Chesson, 1995). Morgan (1998) demonstrated the necessity of canopy gaps for the establishment of some herbs from seeds in tussock grasslands. Possingham *et al.* (1995) suggested that a late-successional species are common colonizers following a tree fall. Trees, whether fallen or erect, can trap the disseminules of wind dispersed species (Carriere, 2002).

Soil moisture is highly influenced by the presence of tree root systems. A negative impact of the trees on soil moisture is also caused by canopy interception. There is a great amount of precipitation trapped by the canopy and evaporated before reaching the ground (Smith, 1974; Westman, 1978). Nevertheless, in foggy environments, trees leaves can induce fog drip (Pook *et al.*, 1991) which may substantially increase soil moisture.

The tree itself may prevent the establishment of other species by releasing allelopathic solutions (del Moral and Muller, 1969; Keeley, 1985; Mandal, 2001). It is difficult to conclusively prove the existence of allelopathy. For

example, Kamara *et al.* (1998) found a growth retardation of plants growing under the tree canopy, but could not conclusively relate this suppression to environmental conditions. They speculated that the suppression was an allelopathic effect of leachates from the tree canopy or toxins released by forest floor decomposition.

Trees may increase or decrease fire intensity depending on the degree of flammability of their living organs and litter components. The relative flammability of the trees may, to some extent, create niches that sustain species coexistence (Possingham *et al.*, 1995).

Litter is important not only for fire but also for nutrient cycling. A substantial amount of nutrients is regularly returned to the soil by means of litterfall. It is a major factor that controls biomass production in vegetated ecosystems (Attiwill, 1994; Keith, 1997; Parrotta, 1999). Some trees have long been known to benefit soil nutritional quality by means of symbiotic interaction with nitrogen-fixing microorganisms (Murray, 2001). Nonetheless, the accumulation of litter can physically inhibit seedling establishment and cause growth suppression of the understorey species (Kirkpatrick, 1997).

The genus *Eucalyptus* has some attributes that make it particularly interesting as the subject of an investigation of the influence of trees on the diversity of their understories. Eucalypts have an open canopy which lets through sufficient light for heliophytes to survive, and have complex interactions with fire in both life and death (Specht, 1970; Kirkpatrick, 1997).

There has been limited research on the role of dominant trees in heterogeneity creating processes in dry eucalypt forests (Kirkpatrick, 1997). *Eucalyptus globulus* grassy woodland in Conningham in Tasmania was selected for the present study as it exhibited a variety of apparently dominant-induced ground layer environmental and vegetation patterns. These included geomorphic and edaphic features associated with the trunk and root systems of the larger trees, apparent differences between the subcanopy and the intercanopy in species composition and abundances, and previously undocumented linear bare patches, named log shadows, associated with the past locations of fallen trees.

The aim of this thesis is to document and explain these patterns, with the research hypotheses being that: (1) *Eucalyptus globulus* creates environmental heterogeneity; (2) this induced environmental heterogeneity is reflected in the species richness of the woodland.

The thesis is largely written in the form of papers, with only a brief general conclusion which addresses the research hypotheses (Chapter 6).

The second chapter of the thesis searches for an explanation of the bare ground in log shadows by contrasting their physical and chemical characteristics with those of adjacent well-vegetated ground.

In the third chapter two questions are asked in relation to the log shadows: Are there species that occur preferentially in the log shadows? Do the soil solutions in the shadows favour the germination of species that preferentially occur in them? The hypothesis is that the species that occur preferentially in shadows are environmentally selected.

The fourth chapter addresses two questions: How do environmental variables (soil total nitrogen, soil available phosphorus, soil organic matter content, and soil fraction composition) vary under the canopy of individuals of *Eucalyptus globulus* of various sizes? How does the floristic patterning of the understorey species relate to this variation?

The focus of the fifth chapter is on the difference between the subcanopy of the tree and the intercanopy area in: (1) the size of the nutrient pool of a range of litter components originating from *Eucalyptus globulus* and animals that consume the trees; (2) their decomposition rates; (3) the nutritional contribution of each litter component to nutrient cycling processes; (4) the seasonality of the above.

CHAPTER 2

The Cause of Log Shadows in A Burned *Eucalyptus globulus* Forest at Conningham, Tasmania

2.1 Introduction

Fallen wood plays an important role in a variety of forest ecosystems. It often increases biodiversity (Jonsson, 2000; Pyle and Brown, 1999) and it is an important habitat for many organisms (Lindenmayer *et al.*, 1999). Some substrate demanding plant species are specifically adapted to exploit the decaying wood environment (Jonsson 2000; Kirby *et al.* 1998). McKenny and Kirkpatrick (1999) demonstrated that regeneration of many vascular plants in wet eucalyptus forest is strongly associated with fallen wood.

Fallen wood is not a major nutrient pool in forest ecosystems (O'Connell, 1997). Fallen wood disintegrates much slower than other litterfall components on the forest floor (Brown *et al.*, 1998; O'Connell, 1997). Therefore, the fallen wood tends to accumulate in various decay stages (Pyle and Brown, 1998) and become a major contributor to the coarse fuel load. This type of accumulation and decay, and most of the literature on the ecological effect of fallen wood, pertains to forests in which fire is a rare event. The effects of fallen wood could be expected to be very different in frequently burnt forests.

The presence of fallen wood during a fire creates a wide variability of heat intensity across the burnt area. Whereas fire burns quickly and at relatively low intensities through areas with only fine fuels, a log laying on the ground may burn more intensively for long periods. This is apparently the case in *Eucalyptus globulus* open-forest at Conningham, Tasmania, where stripes of bare ground (log shadows) lead into the charred ends of fallen logs.

Fire results in a large and sudden addition of nutrients into the soil (Bauhus *et al.*, 1993; Derouw, 1994; Grogan *et al.*, 2000; Lynham *at al.*, 1998; Marafa and Chau, 1999; Overby and Perry, 1996). However, the improved nutrient availability occurs only for a relatively short period and is followed by a depletion of nutrients due to leaching (e.g. Thomas *et al.*, 1999; Thomas *et al.*, 2000). Marafa and Chau (1999) suggested that the effect of fire on soil nutrients disappeared as soon as one year after the fire. Gimeno-Garcia (2000) found that the peak of nutrient loss happens at four months after the fire. These nutrients are highly available to plants. The sooner the plants revegetate the soil the more nutrients will be kept within the system. The presence of plants may facilitate the recovery of the soil to the condition prior to the fire (Neary *et al.*, 1999) by increasing organic matter and disaggregating peds (Yeates and Lee, 1997).

High heat intensity destroys buried seeds and soil microorganisms in the surface layer (Jensen *et al* 2001; Odion and Davis, 2000). The soil microbial community is thought to be a key factor in the recovery of vegetation after fires (Boerner *et al.*, 2000) and is important in rebuilding soil nutrient pools

(Attiwill, 1994; Ross *et al.*, 1997). Although soil microorganism activity is greatly reduced by fire (Jensen *et al.*, 2001; Staddon *et al.*, 1998), the effect does not last long (Grogan *et al.*, 2000). Moreover, to some extent, the presence of charcoal may help microorganisms to enhance humus production (Zackrisson *et al.*, 1996).

The burning of the fallen wood may also result in a substantial change to the physical nature of the soil that, in turn, may play an important role in hindering revegetation. The higher the intensity of a fire the more severe is modification of the physical structure of the soil (eg. Clinnick, 1984; Giovannini *et al.*, 1988). McCaw *et al.* (1997) have demonstrated that high heat intensities and subsequent structural soil change are associated with the burning of fallen wood.

This chapter tests hypotheses related to the persistence of log shadows in *Eucalyptus globulus* open woodland at Conningham. These are that the persistence relates to: the alteration of soil physical properties that influences soil parameters, such as water infiltration rates and soil compaction; the chemical status of the soil becoming a limiting factor as a result of a continuing leaching; an inhibitory effect of the leachate from burnt, decaying fallen logs that reduces the viability of the soil to support plant survival. This chapter tests each of these hypotheses by comparing the characteristics of the log shadows with those of the adjacent well-vegetated ground.

2.2 Study Area

The study site is located in Conningham Nature Recreational Area, Tasmania (Fig.2.1. and 2.2). The latitude and longitude of the park is $147^0$15.2'-$147^0$18.0'E and $43^0$4.7'-$43^0$5.9'S. The elevation ranges from 100-180m above sea level. Shallow brown soils derived from dolerite lay on a moderate to steep northeast to north facing slope. Rainfall in the area is likely to be 600-700 mm per annum, distributed relatively evenly throughout the year. The monthly averages for maximum daily temperature in Conningham range between 12.5 and 21.9^{0}C for July and February respectively. The mean daily minimum temperatures range between 2.2 and 10.7^{0}C for June and February respectively. *Eucalyptus globulus*, with a few *E. pulchella*, emerges from a tussock grassland understorey dominated by *Poa rodwayi* and *Themeda triandra*. The open-forest was affected by the catastrophic bushfires in South-Eastern Tasmania in February 1967 (Wettenhall, 1967) and was burned again in 1986.

2.3 Methods

2.3.1 Field Data Collection

To chose log shadows for investigation the following criteria were employed: (1) They were separated by at least three metres from other bare strips to ensure independence; (2) there was not a living tree or shrub taller than 50 cm

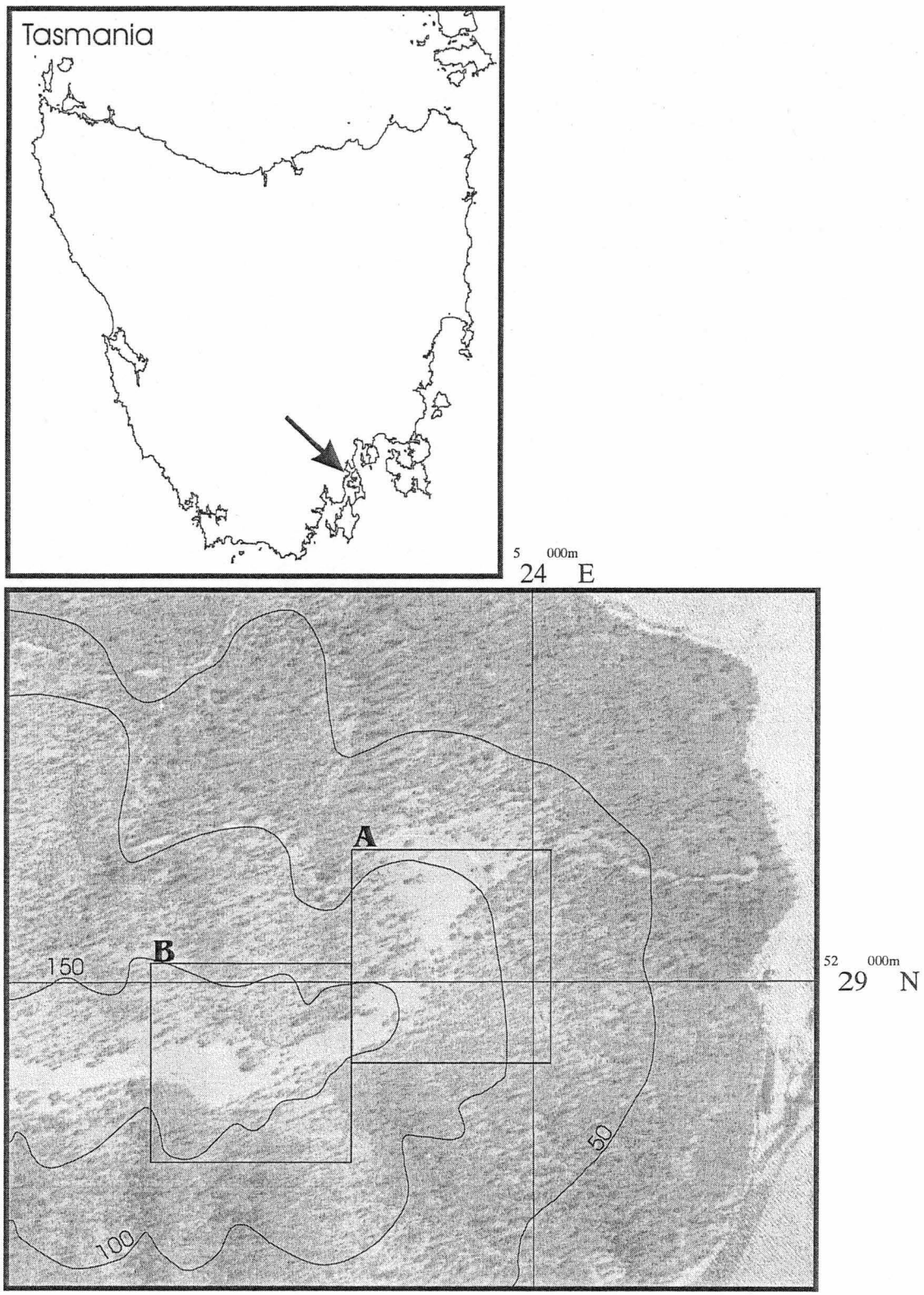

Figure 2.1. Study site location (arrow, upper figure) and a magnification of the site (lower figure). The tree and log shadow distribution is given in Figure 2.2.A and B which corresponds to the areas A and B above.

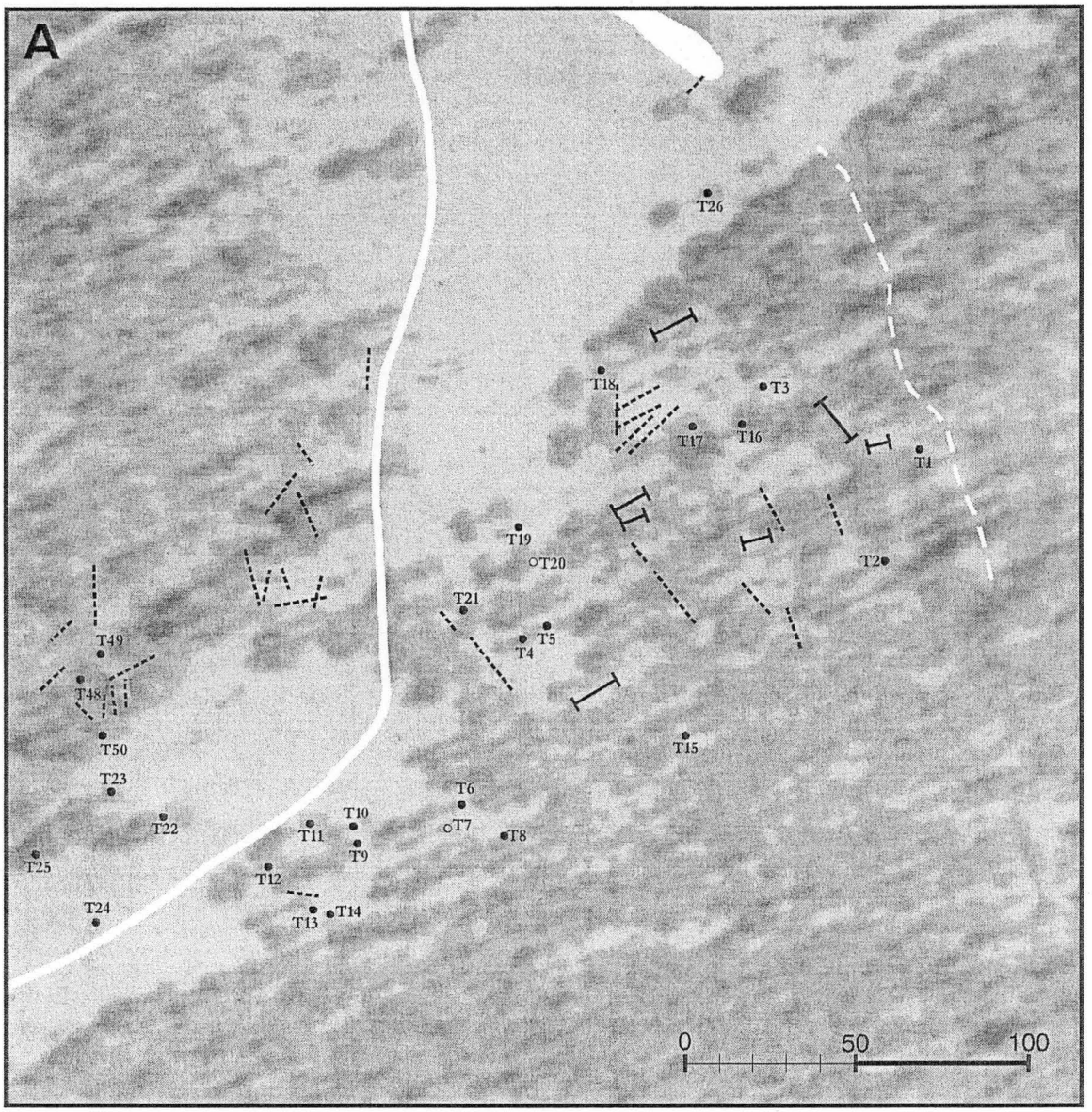

Figure 2.2. Distribution of sampling trees (circles) and log shadows (lines). Solid lines indicate log shadows that were suitable for sampling.

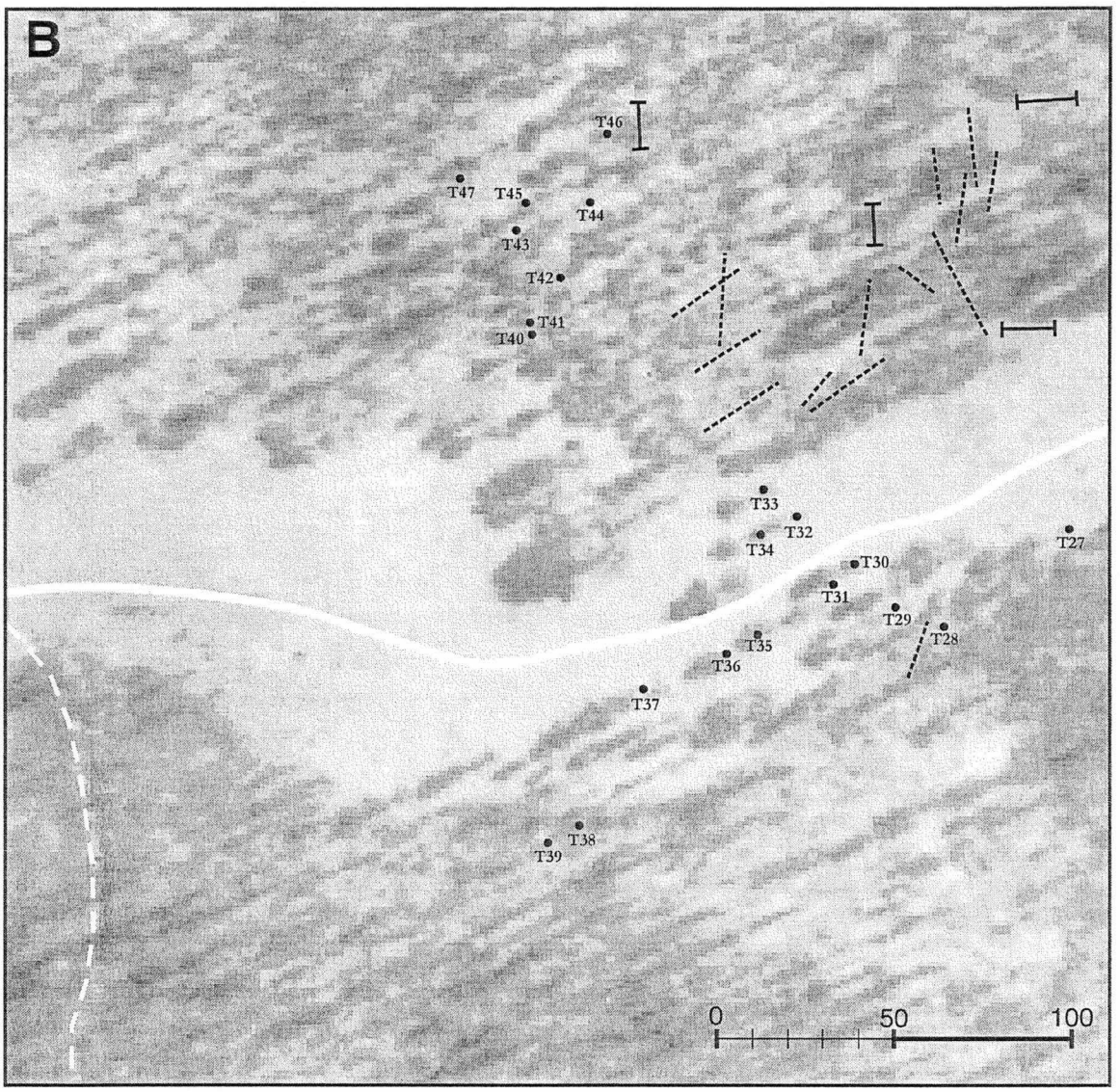

Figure 2.2. (continued)

in the log shadow to avoid interference from the tree in the development of the log shadows; and (3) there was no remaining fallen wood left on the ground since the remaining fallen wood would physically block seed dispersal to the log shadow. Eleven bare patches were found to satisfy these criteria. Five of the shadows lay along the contour and six lay orthogonally to the contour. Those are henceforth called horizontal and vertical shadows, respectively.

As many transects as possible were laid perpendicular to the shadow direction, 75-100 cm apart. There were 62 transects altogether. Transects were 300 cm long and centred at the midpoint of the shadow. The transects were divided into five 60 cm sections to evaluate the similarity or dissimilarity of plant community structure. The first and last sections of the transects are the furthest from the log shadow, the second and fourth sections are adjacent to the shadows. The outline covers of all observable vascular plant taxa were recorded for each of the sections. A line section may exceed 100% total cover caused by overlapping canopies of more than one species. Litter, animal droppings, bare ground and rock cover were also measured. Documentation of plant composition was completed before any soil observations were made.

Measurements of water infiltration and soil penetration resistance in each transect were taken from the centre of the log shadow and from adjacent vegetated ground, the latter alternatively at the left or right extremes of the transect. Sampling of soil for laboratory analysis was done after water infiltration rate and soil penetration resistance were measured. Soil cores of 36 cm^2 with 5 cm depth were sampled. The soil was kept in sealed plastic bags

and immediately taken to the laboratory. Soil samples were spread in plastic trays and air-dried.

Water infiltration rate was measured using a single-ring infiltrometer. The components of the infiltrometer are a water reservoir bottle, a containment ring attached to a bottle holder, a water tube to supply water from the reservoir to the containment ring, a bubble tube, adjustable to control the maximum water level in the containment ring, and a rubber stopper (Figure 2.3). The tubes were tightly inserted through the rubber stopper and then adjusted. The more protruding tube is the water supply tube.

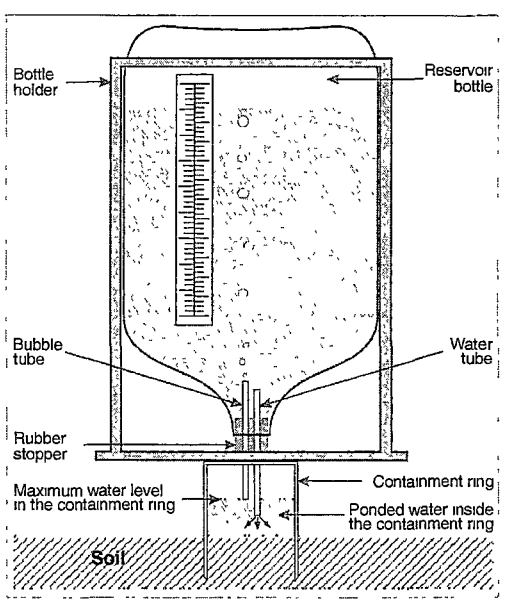

Figure 2.3. Sketch of infiltrometer used for water intake rate

To assess the water intake, the containment ring was carefully pushed into the soil to about 3 cm depth. The water-filled reservoir bottle with the rubber stopper in place was then put into its position. Water filled the containment ring through the water tube. Air escaped through the bubble tube to replace the

amount of water released by the reservoir bottle. When bubbles stopped coming through the tube, that is, when the water level in the containment ring reached the lower end of the bubble tube, a stopwatch was activated. As the soil took in the water, the water level in the containment ring lowered. When the water surface detached the bubble tube, the air for a second time escaped into the reservoir bottle allowing water to flow into the containment ring. When the bubbling stopped, the time and amount of consumed water was recorded. Measurements were taken for three bubbling periods.

Soil penetration resistance was measured using a pocket penetrometer. The piston was gently pushed into the soil until the groove on the piston was level with the soil surface. Readings were taken as the unconfined compressive strength of the soil in $kgf.cm^{-2}$.

2.3.2 Laboratory Analysis

The air-dried soil samples were divided for nutrient, enzyme, and fraction analysis. For nutrient and enzyme analyses soil samples from the same log shadow were combined such that, for each log shadow, there was one sample for the shadow and one for each side of the shadow. When the analysis could not be done immediately, the samples were stored in paper bags.

Soil organic matter was approximated by loss on ignition after heating at $500^{O}C$ for 8 hours. Soil total nitrogen was determined by the Kjeldahl method

and available phosphorus by means of acid extraction, as described by Jackson (1958).

Enzyme activity is an indirect measure of microbial activity (Steinberger *et al.*, 1998). Enzyme activity was measured using the standard methods described by Dick *et al.* (1996) and Tabatabai (1982). 2,3,5-Triphenyltetrazolium chloride (TTC), and triphenyl formazan (TPF) were prepared beforehand. Methanol and calcium carbonate were both reagent grade. TTC 3% was made by dissolving 3 g of TTC in 80 ml water and adjusting the volume to 100 ml. TPF standard solution was made by dissolving 100 mg TPF in 100 ml methanol. TTC and TPF were stored in dark to avoid deterioration. Twenty grams of 2-mm sieved soil was mixed with 0.2 g calcium carbonate ($CaCO_3$, reagent grade). Six grams of the mixture were then put in each of three test tubes. One mL 2,3,5-triphenyltetrazolium chloride (TTC) 3% solution and 2.5 mL distilled water were added to each tube and mixed thoroughly by a glass rod. The tubes were then stoppered and incubated at 37^{O}C for 24 hours. After incubation, reagent grade methanol (10 mL) was added in each tube. The tube was stoppered and shaken for 1 minute. The suspension was then filtered through a glass funnel plugged with absorbent cotton into a 100 mL volumetric flask. All the soil was transferred to the funnel by washing the tube with methanol, and then additional methanol (in 10-mL portion) slowly poured to the funnel until the reddish colour disappeared from the cotton plug. The filtrate was then diluted to 100 mL with methanol. The measurement of reddish intensity was done using a spectrophotometer at 485 nm wavelength and a 1-cm cuvette with methanol as

a blank. The amount of TPF is then determined by referring to a TPF calibration graph. Soil enzyme activity was measured as the extraction of TPF (mg TPF kg^{-1} soil 24 h^{-1}).

The TPF calibration graph was made using the following procedure. One hundred mg TPF in 100 ml methanol was dissolved to make a TPF standard solution. Ten mL TPF standard solution was diluted to 100 mL with methanol (100 mg of TPF mL^{-1}). Aliquots of 5-, 10-, 15-, or 20-mL of this solution (that is equivalent to 500, 1000, 1500, and 2000 mg of TPF 100 mL^{-1}, respectively) were pipetted into 100 mL volumetric flasks which were then filled up with methanol. The red intensity was then measured at 485 nm wavelength. The reading was plotted against the amount of TPF in the 100 mL standard solution to create a standard equation.

Linear regression analysis was used to verify the standard equation for TPF concentration (Y) and the redness (by means of wave absorbance, A) of the standard TPF solution. The analysis produced a linear equation $Y = 0.048 + 0.98A$, with strong correlation coefficients ($R^2 = 0.9988$ and $F < 0.01$). This equation was thus confidently used to estimate TPF concentrations in the solutions extracted from the soil samples.

A modified Buoyoucos hydrometer method of fraction analysis was conducted to measure the proportion of clay, silt, and sand. Thirty grams of air-dried, 2 mm sieved soil were transferred to a 600 mL glass beaker containing 200 mL water. Ten mL of sodium hydroxide (1 N) and 20 mL of calgon (10%) were

added. The solution was then mixed using an electric stirrer for about 10 minutes. The suspension was transferred to 500 ml graduated cylinders which were then filled with distilled water. The temperature was noted and the suspension was shaken vigorously but carefully for one minute. The hydrometer was introduced and timed. Readings to indicate the amount of particles in the suspension were done at the 23rd second and 120th minute following the shake. The measurement at the 23rd second reads silt and clay particles in the suspension, at the 120th minute clay is left in the suspension. Particle sizes were referred to the standard produced by the USDA. It should be noted that the soil organic matter was not secluded from the sample during analysis.

2.3.3 Data Analysis

Dissimilarity of floristic composition between the log shadow and the covered ground at various distances from the shadow was assessed by a multivariate analysis. Ordination of the floristic data was performed using multidimensional scaling (MDS) following the default options in DECODA (Minchin, 1990). The pattern of stress reduction suggested a two-dimensional solution to be the most useful. Paired t-tests were used to detect differences between the bare and covered ground on water infiltration rates, soil compaction, nutrient contents, enzyme activity, and soil fraction composition.

2.4 Results

2.4.1 Vegetation Patterns

The log shadows were floristically distinct from the adjacent well-covered ground, with the ordination scores being well separated in ordination space (Figure 2.4). The separation is more evident on the first (abscissa) axis than the second (ordinate) axis. The direction of log shadows relative to the hill slope influences plant community patterns, in that there is greater differentiation between the two sides of the shadow when it is horizontal (Figure 2.4, Table 2.1).

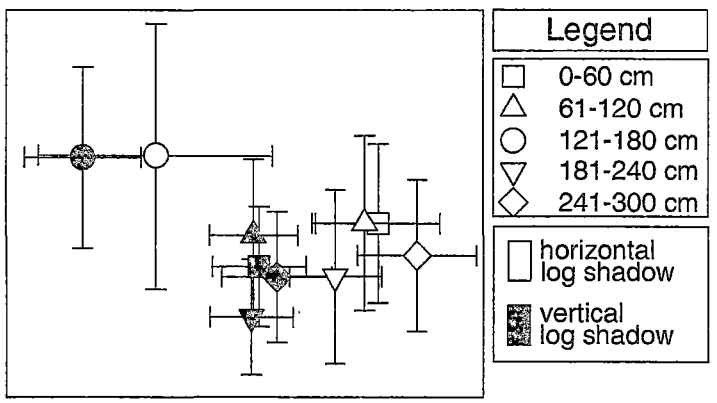

Figure 2.4. Plots of values produced by MDS analysis.
Note: Horizontal and vertical bars represent 95% confidence intervals. The log shadows are centred in the 121-180 cm area.

Table 2.1. Bare soil distribution along the transects

Range (cm) along transect	Horizontal Shadow		Vertical Shadow	
	Position	Bare ground (%)	Position	Bare ground (%)
0-60	Far Down	0.00	Far Left	4.46
60-120	Near Down	16.02	Near Left	9.07
120-180	Middle	94.26	Middle	85.29
180-240	Near Up	14.72	Near Right	6.81
240-300	Far Up	1.85	Far Right	6.32

2.4.2 Soil Characteristics

The log shadows are significantly different from the well-vegetated ground in their proportion of texture classes, especially for coarser soil particles (Figure 2.5). The average of clay particle content in the log shadows was not significantly different from the adjacent vegetated ground (P = 0.1616). The paired t-test, however, shows a significant difference (P = 0.0174) indicating that soil samples from the log shadows persistently contain lower content of clay in comparison to adjacent samples in the vegetated ground. The silt fractions are significantly lower (P = 0.0148) in the log shadow than in the well-vegetated area. A highly significant difference in sand fraction (P = 0.0041) was shown between the log shadows (39.7%) and well-vegetated ground (35.3%).

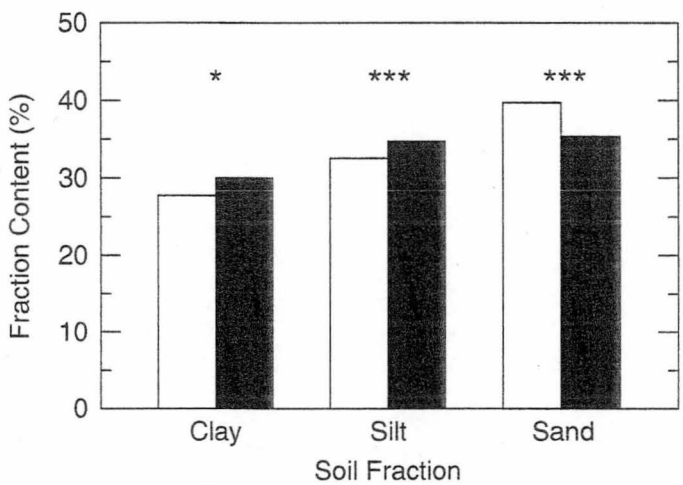

Figure 2.5. Soil fractions in log shadows (blank) and covered ground (shaded).
Note: ns = not significant, *P < 0.05, **P < 0.01, ***P = < 0.001.

Soil in the log shadows appears to be coarser in texture than the well-covered ground with the differences less distinct in the horizontal fallen logs. The average content of sand is significantly higher (P = 0.0094) in the shadows than in the well-covered ground when the shadow is vertical (Figure 2.6). Significance different in clay was also shown only in the vertical log shadow (P = 0.0477). Although the sand fractions were higher in the bare ground of horizontal log than they were in the well-covered ground but the difference is not statistically significant (P = 0.1219).

When the comparison is made between the orientation of the fallen wood relative to slope contour, bare soil in the vertical shadows contain significantly higher sand fractions (P = 0.0185) and lower clay fraction (P < 0.0001) than that in the horizontal shadows (Figure 2.6). Silt content is not significantly different between the log shadows and the well-covered ground.

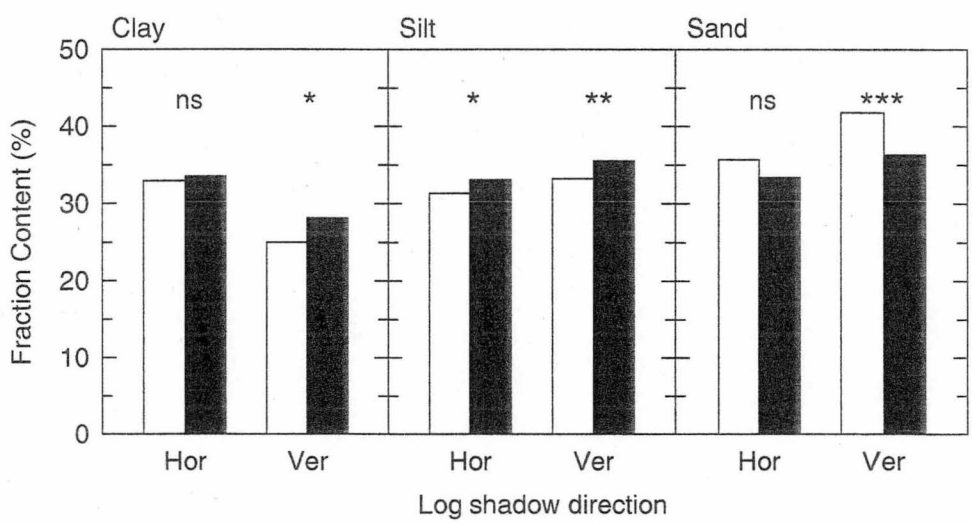

Figure 2.6. Soil fractions in the horizontal (Hor) and vertical (Ver) log shadows (unshaded bars) and vegetated ground (shaded bars).
Note: ns = not significant, *P < 0.05, **P < 0.01, ***P = < 0.001.

Water infiltration rate is higher in the log shadow (0.71 mm sec^{-1}) than in the well-covered ground (0.57 mm sec^{-1}) for the comparison as a whole (Figure 2.7). The difference seems to be persistent as the paired t-test revealed a significant difference between the two (P = 0.0436). Soil in vertical log shadows shows higher infiltration rates (0.75 mm sec^{-1}) than the adjacent vegetated ground (0.57 mm sec^{-1}). The difference is statistically significant only in the vertical log shadows (P = 0.0496). Even though the infiltration rates in the log shadow is higher in the vertical than horizontal shadows, the difference is not statistically significant (Figure 2.8). It is also clear from Figure 2.8 that there is no difference in infiltration rates between the well-covered ground adjacent to the horizontal log shadows.

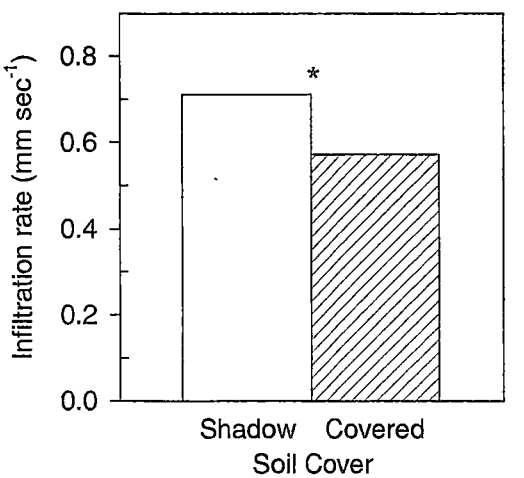

Figure 2.7. Water infiltration rates in the log shadow and well-covered ground.
Note: ns = not significant, *P < 0.05, **P < 0.01, ***P = < 0.001.

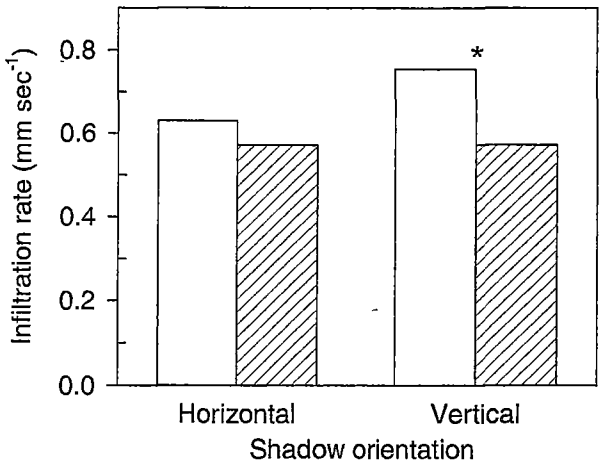

Figure 2.8. Water infiltration rates in the log shadow and well-covered ground (shaded) of the horizontal and vertical oriented logs.
Note: ns = not significant, *P < 0.05, **P < 0.01, ***P = < 0.001.

The penetrometer required an average of 2.15 kgf.cm^2 to penetrate the covered ground and only 1.93 kgf.cm^2 to penetrate the shadow, a difference that was significant (P = 0.0250) (Figure 2.9).

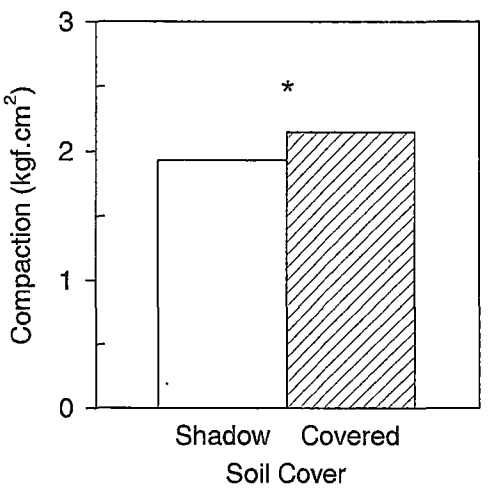

Figure 2.9. Soil compaction in the log shadow and well-covered ground.
Note: ns = not significant, *P < 0.05, **P < 0.01, ***P = < 0.001.

Only log shadows in horizontal orientation showed a significant difference in soil compaction (P = 0.0376) between the shadows and well-covered ground (2.23 and 2.57 kg.cm^2, respectively; Figure 2.10). Soil in the horizontal log shadow is apparently more compacted than soil in the vertical strip whether in the shadow or the well-covered sides (P < 0.01 for both). The magnitude of the difference is more obvious in the well-covered ground (Figure 2.10).

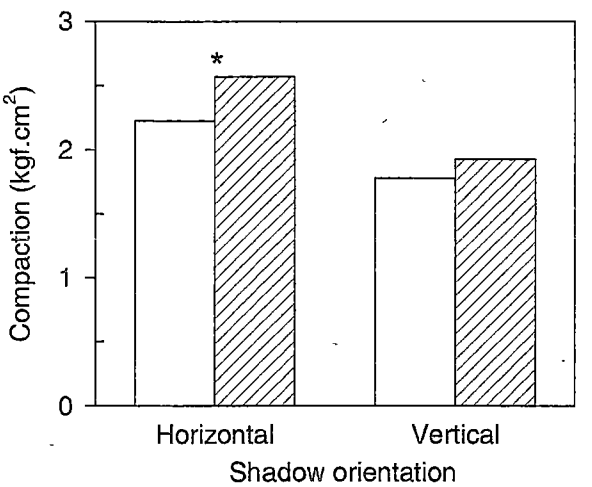

Figure 2.10. Soil compaction in the log shadow and well-covered ground (shaded) of the horizontal and vertical oriented logs.
Note: ns = not significant, *P < 0.05, **P < 0.01, ***P = < 0.001.

Soil organic matter content is significantly lower in the log shadows (10.90%) than in the covered ground (13.76%) (P < 0.0001; Figure 2.11). The lower soil organic matter content in the shadows is found to be consistent regardless the orientation of the log shadows (Figure 2.12). Only the comparison between log shadow and lower vegetated ground was not statistically significant.

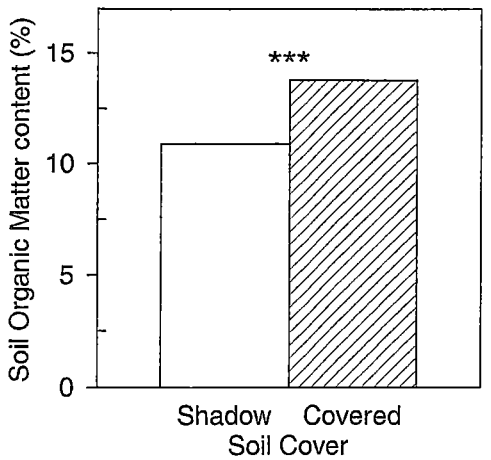

Figure 2.11. Soil organic matter contents in the log shadow and well-covered ground.
Note: ns = not significant, *P < 0.05, **P < 0.01, ***P = < 0.001.

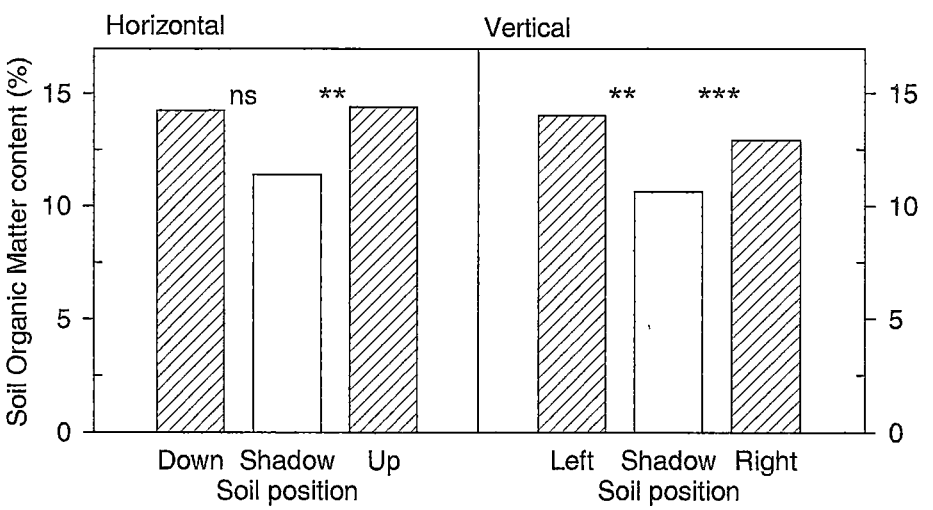

Figure 2.12. Soil organic matter contents in the log shadow (unshaded columns) and well-covered ground (shaded) of the horizontally and vertically oriented logs.
Note: ns = not significant, *P < 0.05, **P < 0.01, ***P = < 0.001.

Soil total nitrogen in the log shadow is generally lower than in either side of the well-covered ground (Figure 2.13). The difference to the left side of the vertical shadow is the only one that is not statistically significant. Soil in the bare ground of horizontal shadows contains only 0.13% total nitrogen in comparison to 0.21% and 0.22% in the well-vegetated ground at the up and

down sides of the log shadow, respectively. The soil total nitrogen of vertical shadows is 0.18%, which is more than a third higher than the horizontal shadow with soil nitrogen only 0.13% but the difference is not statistically significant (P = 0.0921; Figure 2.14).

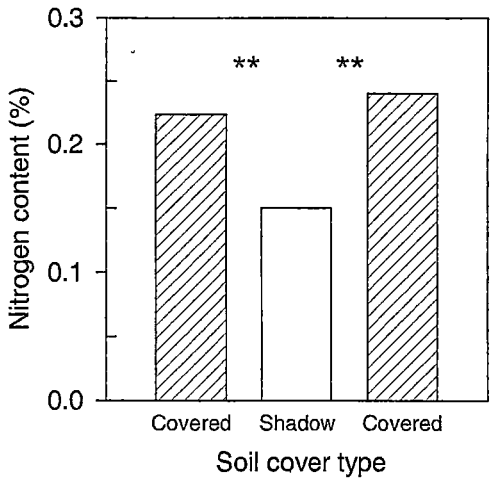

Figure 2.13. Soil total nitrogen contents in the shadow and covered ground.
Note: ns = not significant, *P < 0.05, **P < 0.01, ***P = < 0.001.

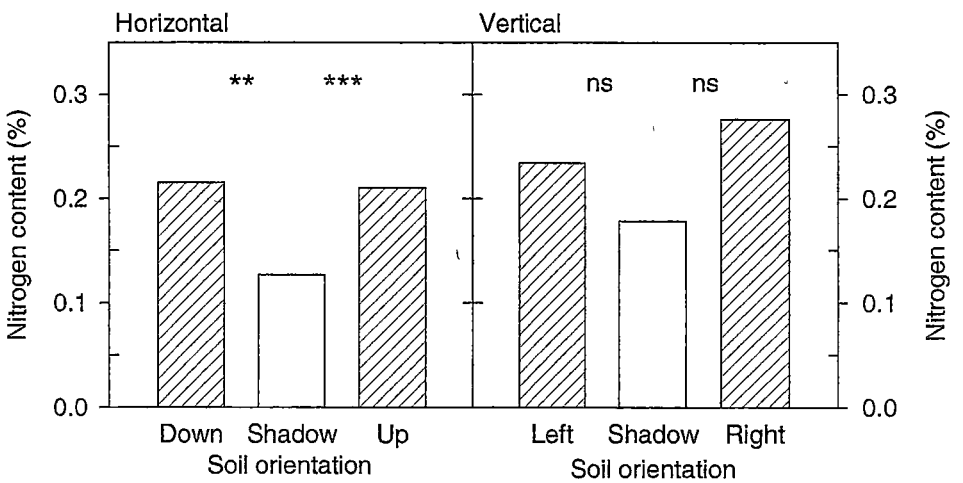

Figure 2.14. Soil nitrogen contents in the log shadow (unshaded) and well-covered ground (shaded) of the horizontally and vertically oriented logs.
Note: ns = not significant, *P < 0.05, **P < 0.01, ***P = < 0.001.

There seems to be a build-up of available phosphorus in the well-covered ground of the down sides of the horizontal log shadows. There is a big gap in the mean available phosphorus between the bare ground of the horizontally oriented log shadows and their down side (3.83 and 6.67 ppm, respectively). The difference, however, is not statistically significant (Figure 2.13). There is no significance difference between the log shadow and the upper, well-covered side.

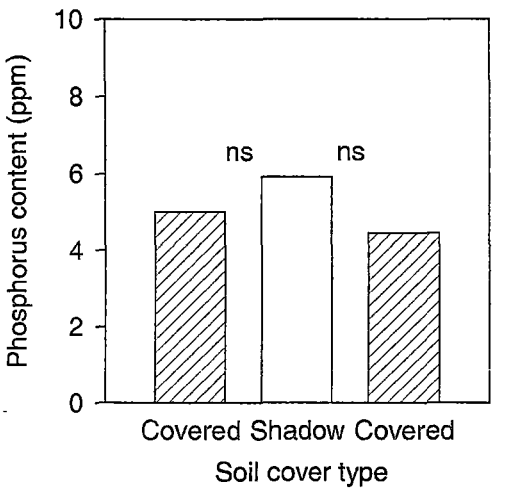

Figure 2.15. Soil available phosphorus in the log shadow and covered ground.
Note: ns = not significant, *P < 0.05, **P < 0.01, ***P = < 0.001.

Soil available phosphorus in the vertical shadows shows a pattern contrary to the soil total nitrogen (Figure 2.16). The soil available phosphorus in the bare ground of the vertical shadow (8.40 ppm) is significantly higher than the well-covered ground both on the left side (3.20 ppm; P = 0.004) and right side (4.20 ppm; P = 0.0314). The average soil available phosphorus of 8.40 ppm in the bare ground of vertical log shadows is markedly higher than that of the horizontal log shadows (P = 0.0007).

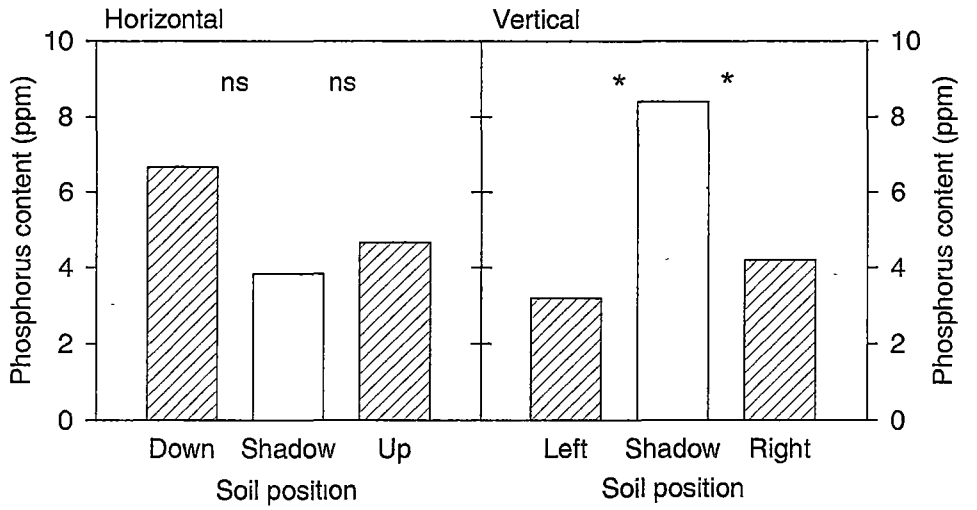

Figure 2.16. Soil available phosphorus contents in the log shadow and well-covered ground (shaded) of the horizontally and vertically oriented logs.
Note: ns = not significant, *P < 0.05, **P < 0.01, ***P = < 0.001.

Figure 2.17 shows a significantly low microbial activity in the log shadows in comparison to the well-vegetated ground as a whole (P-values < 0.5). As a matter of fact, microbiological activity in the well-vegetated ground (15.83 and 17.65 mg TPF kg^{-1} soil $24\ h^{-1}$) is more or less double the activity in the bare ground (8.65 mg TPF kg^{-1} soil $24\ h^{-1}$).

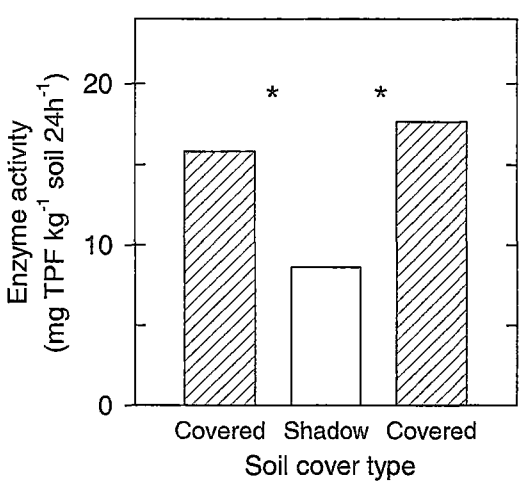

Figure 2.17. Soil enzyme activity in the log shadow and well-covered ground.
Note: ns = not significant, *P < 0.05, **P < 0.01, ***P = < 0.001.

The difference is not significantly demonstrated when the log shadows are examined according to their orientation relative to the contour lines (Figure 2.18). The paired t-test shows a greater probability that there is a difference between the horizontal log shadows and their adjacent covered grounds. The difference is not statistically significant, however, with P-values of 0.0905 and 0.0620 for the comparison of the log shadow to the lower and upper sides of the shadows, respectively.

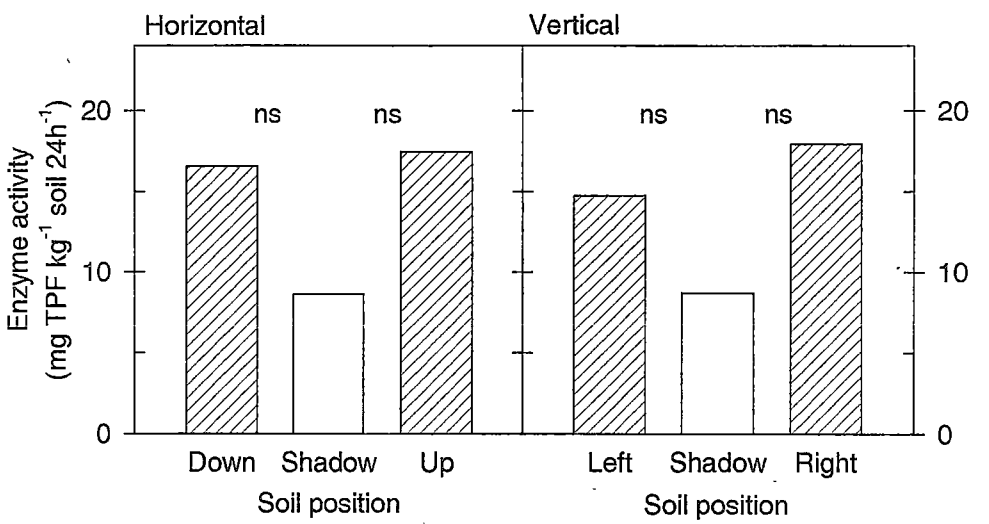

Figure 2.18. Soil enzyme activity in the log shadow and well-covered ground (shaded) of the horizontal and vertical oriented logs.
Note: ns = not significant, *P < 0.05, **P < 0.01, ***P = < 0.001.

2.5. Discussion

The recovery of plant cover following fires is affected by the presence of fallen logs prior to the fire. Plant species composition in the relatively bare log shadow is floristically distinct from the neighbouring vegetated ground that presumably has experienced not only an equal time elapsed since the fire but

also the same climatic conditions. There are several possible causes of persistence of bareness including the high heat intensity of the fire that brings about sterilization of soil surface and the alteration of soil physical and chemical nature of the soil, and/or the inhibitory effect of the leachate from burnt, decaying fallen logs.

The sterilization of the surface soil seed bank seems unlikely to be the cause of the shadows since the severest effects of fires on seed banks has been shown to persist for only two to five years after fire (Fayos, 1997; Schimmel and Granstrom, 1996). The bare patches studied in Conningham have persisted for at least 13 years. Given that the bare patches were surrounded by a luxuriant tussock grassland and were within dispersal distance for tree seeds, seed source should not have been a limiting factor (Galipeau *et al.*, 1997). In grassland, the fire must have been light to moderate. An experiment by Franklin *et al.* (1997) in a quercus dominated community found that light to moderate fire raised the surface soil temperature from 52 to 260 ^{0}C. At this level of heat, fires have little effect on vegetation composition (Franklin *et al.*, 1997).

Soil texture is a physical characteristic of the soil that is thought to vary as a result of variations in fire intensity. Under burning logs the heat intensifies and may increase to more than 800^{0}C, as indicated in Odion and Davis (2000). Giovannini *et al.* (1988) found that heating at 220 ^{0}C and above sharply increases the sand fraction and decreases the silt and clay fractions. A decrease in clay content is a common observation in a fire-affected soil (Fayos, 1997;

Hall, 1996; Ketterings *et al.*, 2000; Ulery and Graham, 1993), because as heating proceeds aggregation of finer particles into larger particles occurs (Clinnick, 1984; Fayos, 1997; Giovannini and Lucchesi, 1997; Giovannini *et al.*, 1988). This process is irreversible at 400^0C or above (Clinnick, 1984). It may be comparable to the burn-bare intensity proposed by Craig (1968). Beyond 400^0C there is no significant increase in soil aggregation.

These textural changes were evident in the study area with the coarse soil particles being significantly greater in the log shadow than in the adjacent grassland. This coarse-structured soil might have been a main factor in the persistence of soil bareness in the early years after the fire. As a result of soil sterilization under the intensive fire under the log, some delay in vegetation recovery could be expected from the lack of soil-stored seed. However, given that shortly after fire the adjacent ground had been fully revegetated, the potential for recovery from seed and/or perennating organs can be assured to have been high. The fact that this did not accelerate colonization and recovery supports the idea that the delay in recovery was caused by soil conditions.

The variation in soil texture with direction of logs in relation to slope suggests the important role of rainfall in amplifying the alteration of soil textural composition following the fire. It is evident that there was a marked lower level of finer particles in the vertical log shadows, compared to the horizontal log shadows. The fact that the horizontal shadow can maintain the same clay content as the adjacent vegetated ground indicates that there may be a constant supply of finer particles from the vegetated, upper-side ground adjacent to the

shadow. This process may be comparable to the sediment capture and retention by grasses proposed by Tongway and Hindley (1995).

The measured mean infiltration rate in the log shadows was 2556 mm/hour (0.71 mm sec^{-1}), much higher than the 200-mm/hour rate reported by Hester *et al.* (1997) for the unburnt oak-dominated sites (only 129 mm/hour in the burnt soil), possibly a reflection of differences in the length of the measurement period before the soil reached saturation. Therefore, the infiltration rates here are only useful for comparison within this study.

The results of the present study suggest that the infiltration rates are higher in the log shadows where the coarser soil is found. An increase in water infiltration rates in soil subjected to fire has been also reported by Fayos (1997) and Soto and Diazfierros (1997). It may be associated with the formation of macropore space and larger soil aggregates during the fires (Boyer and Miller, 1994; Clinnick, 1984; Fayos, 1997). Not only does coarser soil pass water more easily, it also tends to have a low capacity to retain water (Clinnick and Willatt, 1981; Clinnick, 1984). The formation of coarser soil, therefore, is disadvantageous to the recovery of vegetation.

Nevertheless, the results of present studies seem to contradict the results of those who reported a decrease in the soil infiltration rate after fire (Craig, 1968; DeBano *et al.*, 1977; and Hester *et al.*, 1977). The reason for the reduction in water infiltration in those studies was the creation of a water

repellent layer, which is steadily washed away from the soil surface and is most likely to disappear by about four months after fire (Andreu, 2001).

Orientation of log shadows influences the patterning of infiltration rates and soil compaction. The higher water infiltration rates of the soil in vertical log shadows coincide with a markedly higher sand fraction. This strengthens the arguments on the capacity of vertically oriented log-shadow to allow rain water to wash finer soil particles from the shadow. In the horizontal log shadows, the leachate or washed finer particles from the upper side of the shadow makes its way downhill through the shadow. The vegetation in the lower part of the shadow may act as a buffer to trap the flow (Gandolfi and Savi, 2000). This trapping mechanism is confirmed by the significant accumulation of clay particles in the downside of the log shadow and also by a more balanced proportion between the three soil fractions in the horizontal log-shadows compared to the vertical log-shadows, which have much less clay (Figure 2.6).

Patterning of soil compaction reverses the patterning of water infiltration rates. Soil in the log-shadows with its coarser texture is less compacted than the well-covered soil, which is generally finer in texture. Assuming that fire-impacted soil was compacted by the fire (Iglesias *et al.*, 1997), the present state of compactness may relate to the loss of clay fractions from the soil. The presence of vegetation may play a role in adding soil hardness.

The low soil organic matter content in the log shadow may have been a direct consequence of high intensity burning of the fallen wood (Bird *et al.*, 2000; Derouw, 1994; Fernandez, 1997; Marafa and Chau, 1999; Roscoe et al., 2000). It may also be caused by a short supply of organic material from the vegetation. The low quantity of soil organic matter in the log shadows may have come mainly from the litter fall blown from the adjacent ground, and from the remnant of the burnt organic particles. This low organic matter is unfavourable for plant recovery as it affects nutrient availability in the soil. In the present study, the variability of soil total nitrogen closely resembles the pattern of soil organic matter confirming that the soil organic matter is probably the main source of nitrogen. The continuity of nitrogen availability in the log shadows must have been ensured by the surrounding vegetation. The relative lack of soil organic matter, and as a result also nitrogen, may therefore be a reason for the bareness in the log shadow.

However, soil in the log shadow is markedly higher in available phosphorus than the soils in well-vegetated ground, especially when the log-shadow is vertical, that is, where the prolonged impact of the burnt fallen wood is the most extreme. Phosphorus adsorbed to soil particles could be easily mobilized, and made available to the plants, if there is water to dissolve and carry it. Since the water availability is in question in the given soil, the richly available phosphorus may not aid plant recovery in the log shadows. In contrast to a report by Handreck (1997), soil with high phosphorus availability may not promote rapid establishment of fire ephemerals and tree seedlings. In the log shadow the reasons may be twofold, firstly, the unbalanced ratio to other

nutrients (i.e. nitrogen) and, secondly, a lack of sufficient moisture for the survival of newly arrived plants.

The appreciable amount of phosphorus in the log shadow may have been released from the soil, and the combustion of organic material, in a high intensity fire (Clinnick, 1984; Cass *et al.*, 1984; Johnston and Elliott, 1998; Overby and Perry, 1996) and conserved in the log shadow since the fire. Rain might caused leaching of available phosphorus because of the weak binding of sorbed phosphorus in a fire-affected soil (Romanya *et al.* 1994), but phosphorus is easily immobilized on the soil colloids (Clinnick, 1984) so the loss of phosphorus by leaching is usually very low (Buckman, 1969; Hall, 1996; Thomas, 1970). Lynham *et al.* (1988) and Tolhurst *et al.* (1992) reported an increase in soil phosphorus after fire that continued for five to ten years.

Low rainfall restricts the leaching of phosphorus (Sposito, 1989). There is evidence of mobility of phosphorus at Conningham. A significant amount of phosphorus remaining in the vertical log shadows contrasts with the low phosphorus content in the horizontal log shadows. The phosphorus may have been washed from the horizontal log shadows to the lower side of the shadow. The evidence is not convincing since the difference in phosphorus content between the log shadows and the vegetated ground at the down side of the shadow is not statistically significant.

Soil microorganism activity may reflect a succession after fire (Boerner *et al.*, 2000; Staddon *et al.*, 1998), the presence of charcoal (Pietikainen *et al.* 2000; Zackrisson *et al.* 1996), soil water content (Luo *et al.*, 1996), soil structure (Curci *et al.*, 1997; Haring *et al.*, 1994), and soil nutrients (Johnson, *et al.* 1999). Given that the well-covered ground is highly proximal to the log shadows, distance presents no great dispersal obstacle (Theodorou and Bowen, 1982). The fact that microbiological activity in the log shadows was much less than it is in the well-covered ground in Conningham may be the result of soil sterilization by intense fire (Renbuss *et al.*, 1973), colonization being prevented by the dryness induced by soil physical change (Luo *et al.*, 1996) to a coarse structured soil. Renbuss *et al.*, (1973) reported that when soil is kept watered, the recovery of soil microbial population can be achieved in less than a year, even after a high intensity fire. Therefore, the low microbial activity in the soil may be the result of persistent bareness.

Low rainfall at Conningham may exacerbate the effects of the intensive burn under the fallen wood (Figure 2.19). Rainfall was especially low during the study period, with the calculated difference between field capacity and soil moisture (the Soil Dryness Index, SDI, Mount, 1972) being unusually high. When rainfall is low the soil in the log shadow may not have sufficient moisture for sufficient time to allow seedling establishment (c.f. Jacqmain *et al.*, 1999; Totoev and Kleeman, 1998). It highlights the critical inability of plant species to cope with seasonally extreme conditions, and to survive in a severely burned soil, even if it is just the size of a fallen tree.

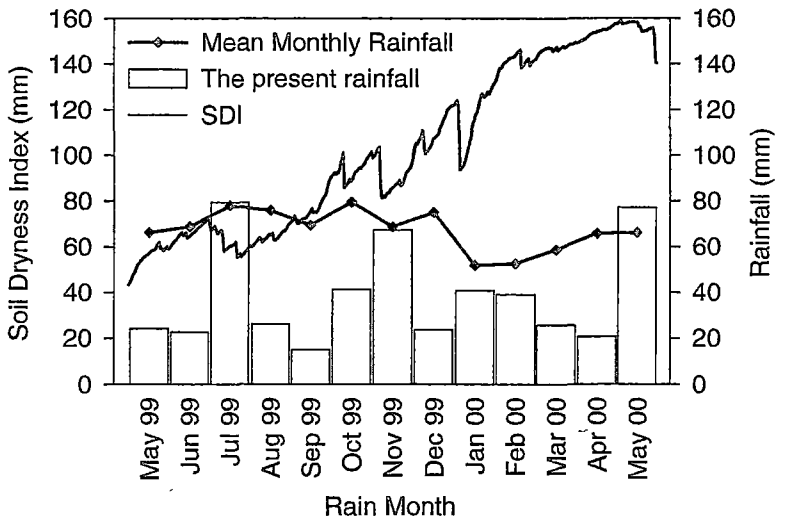

Figure 2.19. Rainfall and Soil Dryness Index (SDI) at Snug, near Conningham.
Note: SDI illustrates the amount of water required to bring the soil water content to field capacity.

Low biological activity in the log shadows is not consistent with the pattern of soil nutrients. Soil sterilization and limitation in seed dispersal are unlikely to be the cause of bareness given (1) the relatively long time after the fire and (2) the close proximity of the bare ground to the adjacent vegetated ground. The physical nature of soil, including the soil fraction composition, soil compaction, and water infiltration rates, indicates that the log shadows have a limited capacity to retain water. It is concluded that the burning of fallen logs generates soil conditions antagonistic to plant recovery after the fire. The orientation of the log shadows seems to make a difference in speed of revegetation. The horizontally oriented log shadows trap phosphorus and finer soil particles and regenerate faster than vertical log shadows. Low rainfall may play a significant role in preserving log shadows in the forest landscape.

CHAPTER 3

Persistent Species Composition Differences Related to The Persistent Effects of Differences in Fire Intensity on Soils

3.1 Introduction

The physical differences between log shadows and adjoining well-vegetation ground documented in the previous chapter have persisted for at least 13 years. In other studies, where physical differences have been observed as a result of differences in fire intensity, these differences have been associated with differences in species composition (Clinton *et al.*, 1996; Guo, 2001; Lloret, 1998; Lynham *et al.*, 1998; Schimmel and Granstorm, 1996; Tyler, 1995). In some cases these floristic differences have been experimentally shown to relate to the differential responses of individual species to the nature of the two adjacent environments (Hahs *et al.*, 1999; Tolhurst *et al.* 1992; Tyler, 1996).

Clarke and Davidson (2001) found that the emergence of some trees and shrubs of temperate woodlands is improved by intense heating although they related the time of emergence to rain. Intense heating promoted growth in a shade intolerant species, *Anandenanthera colubrine,* (Kennard and Gholz, 2001), and a shade tolerant red fir (Chappell and Agee, 1996). It increased species richness and seedling emergence from a seed bank of heathy *Eucalyptus* woodland (Enright *et al.*, 1997).

The effect of ashbed on plants also varies. Ash was found to be beneficial to the growth of *Eucalyptus regnans* seedlings (Ashton and Kelliher, 1996), but inhibited the germination of *Eucalyptus globulus* although not in solute form (Reyes and Casal, 1998).

This chapter addresses two questions in relation to the log shadows: Are there species that occur preferentially in the log shadows? Do the soil solutions in the shadows favour the germination of species that preferentially occur in them? The hypothesis is that the species that occur preferentially in shadows are environmentally selected.

3.2 Methods

Fifty two, three metre, transects were laid across the log shadows to record plant cover by means of line intercept with the 1.5 m point being the centre of the shadow. The outline covers of all plant species found along the line were recorded to the nearest centimetre. These data are depicted as average cover from the centre of the log shadows, the averages being calculated for centimetre segments.

Seeds of plant species that represent various functional groups were selected to study the effect of soil solutions from bare and vegetated grounds on germination. All seeds for this experiment were collected from the study site

except for *Austrodanthonia caespitosa*, which was collected from other sites of similar nature due to a lack of seed at the site at the time of collection. Seven species were selected: *Poa rodwayi, Agrostis* sp., *Cassinia aculeata*, *Austrodanthonia caespitosa*, *Eucalyptus globulus*, *Ozothamnus purpurascens*, and *Themeda triandra.* Various numbers of seeds were placed in Petri dishes, depending on the size of the seeds. One hundred seeds were used for *Poa rodwayi*, *Agrostis* sp, *Cassinia aculeata*, *Eucalyptus globulus*, and *Ozothamnus purpurascens*, 80 seeds for *Austrodanthonia caespitosa*, and 50 for *Themeda triandra.* Seeds were laid on layers of filter paper and kept at a constant 20°C temperature in a dark growth chamber. After the designated 30 days germination period, *Themeda triandra* did not germinate. The temperature was increased to 30°C and the germination period was extended to 50 days. Water was collected after passing through the soil from bare and vegetated ground and applied to the germination medium as long as needed to keep the medium just moist all the time. Ten Petri dishes were employed for each treatment and for each species. Three Petri dishes were used for each species to monitor the germination rate of untreated germinating media. There was a total of 23 Petri dishes for each species. Distilled water was used to keep the media moist. The effects of treatments at 5, 10 and 30 days after sowing were tested using ANOVA. Differences between treatments were analysed using the Pairwise Multiple Comparison Procedures of Student-Newman-Keuls.

3.3 Results

3.3.1 Distribution of Species

Distinct distribution patterns among the most abundant species can be recognized (Figure 3.1). *Poa* spp. (comprised mainly of *Poa rodwayi*) has an inverse distribution to bare ground, with low cover in the log shadows. *Themeda triandra* also shows an avoidance of the log shadows. The degree of avoidance is stronger than that of *Poa*. The presence of *Themeda triandra* gradually increases as the distance from the log shadows increases. *Austrostipa* spp. have relatively high cover in the log shadows, which variably declines in the well-covered ground. This taxon is most abundant in the transition between the log shadows and well-covered ground. *Bossiaea prostrata* is not present in the bare ground, has low cover in the transitional zone, and continually increases into the well-covered ground. *Lomandra longifolia* shows another pattern. It avoids log shadows but peaks at their edges.

The distribution of species in the lower range of abundance (frequency of abundance between 5 and 10%) also shows variable patterns (Figure 3.1). *Austrodanthonia caespitosa* preferentially occurs in the log shadows but can also variably be found in the well-covered ground. To some extent *Plantago varia*, *Austrostipa aphylla*, and *Astroloma humifusum* are down-scale replicas of *Poa* spp. The frequency distribution of the graminoid, *Dianella revoluta* is

similar to that of *Lomandra longifolia*. It avoids the log shadows but tends to establish near them.

The patterns of avoidance and preference are apparent also in species with frequency of occurrence between 1 and 5% (Figure 3.1). *Ozothamnus purpuracens* and *Dichelachne rara* preferentially occur in log shadows or in the transitional zone. *Opercularia varia* and *Oxalis perennans* do not exhibit a particular site preference. *Linum marginale*, *Gonocarpus tetragynus* and *Wahlenbergia* spp. may represent species that preferentially occur in the transitional zones. *Kennedia prostrata*, *Pimelea humilis, Plantago lanceolata, Lepidosperma laterale* and to a lesser extent *Schoenus apogon* and *Geranium* spp. avoid the log shadows.

Confidence in interpreting species preference for log shadows lessens for species with a very low frequency of occurrence (1-2%). No taxon has an obvious preference for log shadows. Some species avoid log shadows (*Carex breviculmis*, *Senecio quadridentatus*, *Euchiton* spp., *Acaena echinata, Goodenia lanata*, *Cynoglossum suaveolens, Olearia ramulosa, and Senecio glomeratus*). Among them *Olearia ramulosa* and *Euchiton* spp. have a tendency to be more abundant in the transitional zone between the log shadow and well-vegetated ground. There are species that were found only rarely (frequency of occurrence <1%). Among them *Crassula sieberana* was exclusively found in the shadow. *Agrostis aemula*, *Lissanthe strigosa*, *Pterostylis* spp., and *Agrostis* spp. were found in both the shadow and well-covered ground. *Ehrharta distichophylla*, *Galium* spp., *Trifolium* spp., *Daucus*

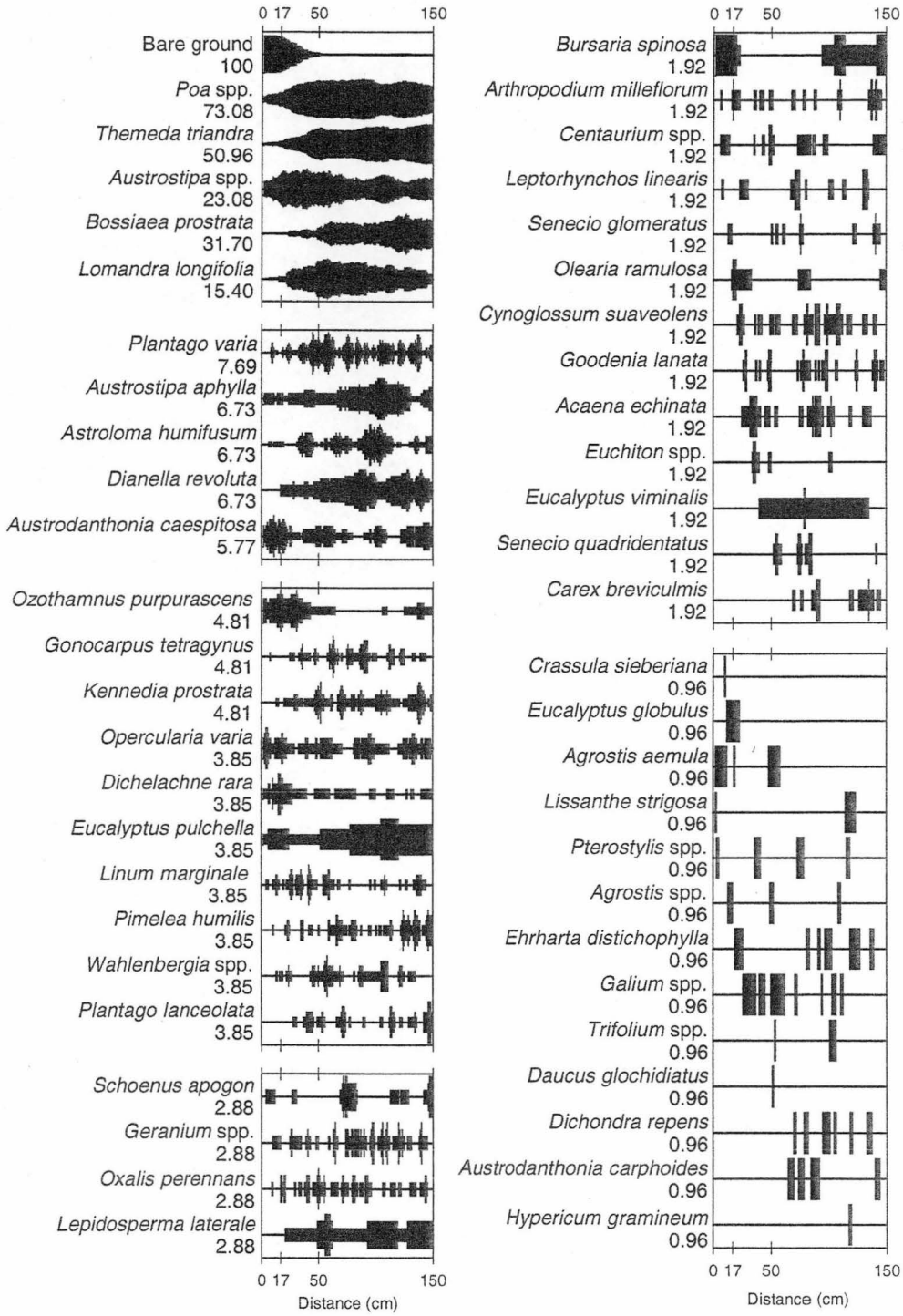

Figure 3.1. Frequency distribution of plant species in log shadows and the adjacent grounds with distance from the center of the shadows.
Note: Numbers indicate maximum frequency of occurrence (%). The vertical axis is frequency expressed as a proportion of maximum frequency.

glochidiatus, *Dichondra repens*, *Austrodanthonia carphoides* and *Hypericum gramineum* were not found in the log shadows.

Seedlings of three eucalypt species found in the study sites show different patterns of distribution in relation to the presence of log shadows. *Eucalyptus globulus* emerged only in the log shadows while *Eucalyptus viminalis* was not found in the log shadows. Seedlings of *Eucalyptus pulchella* were found, to a greater degree than the other two, to emerge from both the log shadow and the well-covered ground.

3.3.2 Germination Experiments

Total germination of *Eucalyptus globulus* seeds in the distilled water control was 91.1%. It is not significantly different to the germination in solution from the log shadow and vegetated ground (90.3 and 89.4%, respectively). An equivalent of 82-87% of the germinants watered with soil solution had already germinated by day 5 compared to only 72% in the control water. The germination was 78.8%, 73.2% and 65.6% in log shadow solution, vegetated ground solution and control, respectively. The difference was not statistically significant ($F = 3.34$, d.f. = 22, $P = 0.0558$).

Treatment with the soil solution from the log shadow persistently showed a positive impact on *Agrostis* germination but the effect was not statistically significant ($F = 0.640$, d.f. = 22, $P = 0.5376$). Total germination was 83.4%

and 82.1% in the solution from bare and vegetated ground, and 76.8% in the distilled water.

Austrodanthonia caespitosa showed significant variations in germination at 15 and 20 days (Figure 3.2). At 15 days there was significantly greater germination in the distilled water control than in either treatment ($F = 4.46$; d.f. $= 22$; $P = 0.0251$), while the germination rates in the solution from well-vegetated ground and log shadow were not significantly different. At the 20 days the solution from log shadow gave a significantly lower germination ($F = 4.71$, d.f. $= 22$, $P = 0.0211$). Germination in the solution from well-vegetated ground was not significantly different to the distilled water.

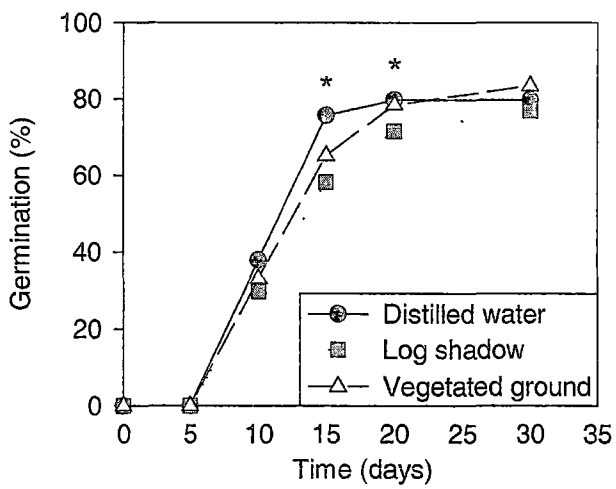

Figure 3.2. Germination of *Austrodanthonia caespitosa*.
Note: Asterisks indicates significant difference at P-values <0.05

The germination of *Poa* seed was also significantly affected by the treatments (Figure 3.3). Solutions from the log shadow and vegetated ground significantly increased germination at 10 days with a stronger influence shown by the solution from the log shadow ($F = 6.14$, d.f. $= 22$, $P = 0.0083$). The

difference between solution treatments weakened at day 15 but germination of *Poa* seeds treated with the solutions was higher than in the distilled water control ($F = 5.50$, d.f. = 22, $P = 0.0125$). The difference in germination became negligible as the germination curves levelled off.

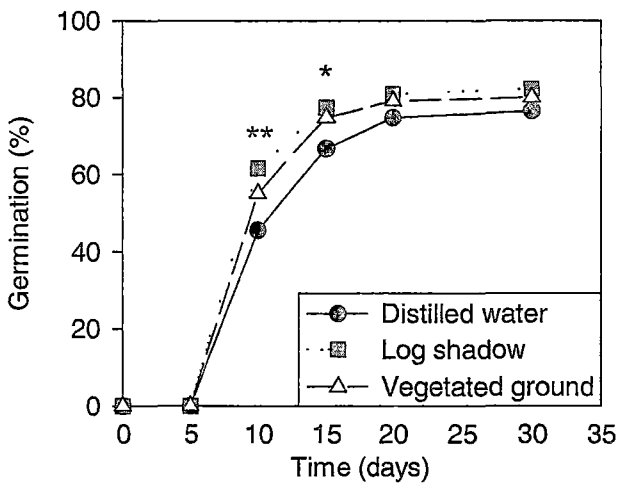

Figure 3.3. Germination of *Poa rodwayi*.
Note: Asterisks indicates significant difference at P-values <0.05 (*) or <0.01 (**).

Themeda triandra seeds germinated after temperature was increased to 30°C after a 30-day attempt to germinate them at a lower temperature. The germination of seeds treated with the soil solutions was significantly lower than the seeds wetted with distilled water starting at the 39th day ($F = 8.17$, d.f. = 22, $P = 0.0025$) and continuing to the 50th day ($F = 5.91$, d.f. = 22, $P = 0.0097$) when the experiment was terminated (Figure 3.4). There was no significant difference between the soil solutions.

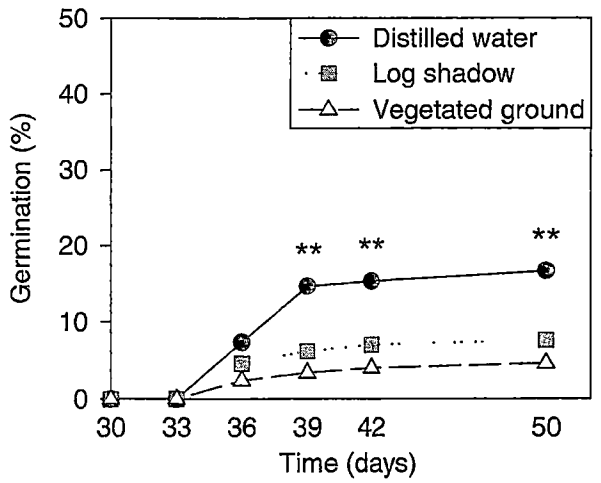

Figure 3.4. Germination of *Themeda triandra*.
Note: Asterisks indicates significant difference at P-values <0.05 (*) or <0.01 (**).

Germination of *Cassinia* seeds treated with the solution from the log shadow soil was significantly higher than seeds treated with the solution from the vegetated ground at day 10 (Figure 3.9; F = 17.8, d.f. = 22, P <0.0001). Germination in both solutions was significantly higher than in the distilled water. At day 15 the difference between soil solutions was not significant but the difference with distilled water continued (F = 9.59, d.f. = 22, P = 0.0012). The germination of *Cassinia* seeds in the control treatment continued to increase and topped the other treatment by the 20th day. At the 20th day of germination the difference between distilled water and the solution from log shadow was not significant while the solution from the vegetated ground was significantly lower (F = 7.72, d.f. = 22, P = 0.0003). To a lesser degree the difference continued to the 30th day (F = 3.60, d.f. = 22, P = 0.0463).

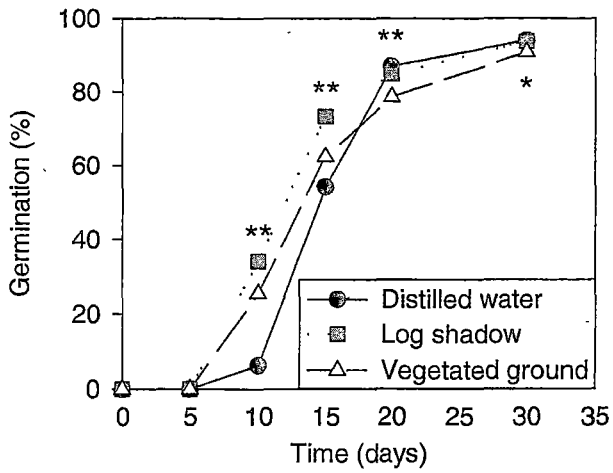

Figure 3.9. Germination of *Cassinia aculeata*.
Note: Asterisks indicates significant difference at P-values <0.05 (*) or <0.01 (**).

Germination of *Ozothamnus* was significantly positively affected by the solution from the log shadows at day 15 (F = 10.3, d.f. = 22, P = 0.0008), while the solution from the vegetated ground did not show a significant difference from the distilled water. The pattern continued to the 20th (F = 26.9, d.f. = 22, P <0.0001) and 30th days (F = 41.2, d.f. = 22, P <0.0001).

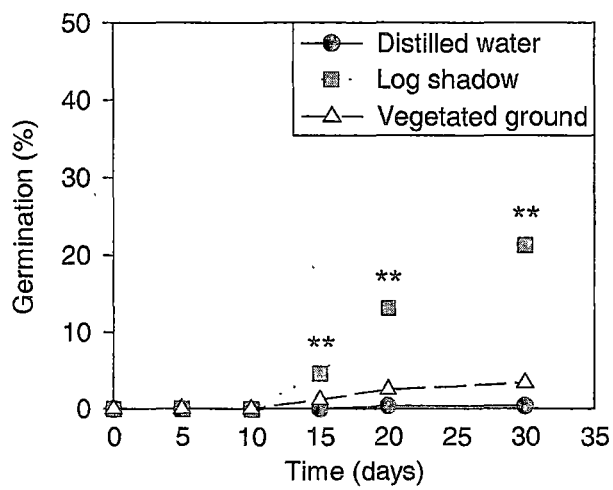

Figure 3.10. Germination of *Ozothamnus purpurascens*.
Note: Asterisks indicates significant difference at P-values <0.01 (**).

3.4 Discussion

The soils in the log shadows are generally richer in nitrogen, are variable in phosphorus and poorer in water retention than the soil of the well vegetated ground (Chapter 2). Some species occurring in the log shadows may be responding to these soil characteristics. For example, *Poa* is better adapted to soil of high nitrogen content than *Themeda* (Groves et al., 1973) reflected in the higher relative abundance of *Poa* than *Themeda* in the log shadow.

Figure 3.11 summarizes the patterns of preferentiality of species used in germination experiment. *Eucalyptus globulus* is not plotted as it is located too far to the right at coordinate 33.9;1.0., a strong log-shadow colonizer, with no preference for either type of soil solution. *Cassinia aculeata* was not found in the transects, so there is no data for the X-axis. Nevertheless, it shows a preference for the log shadow with germination ratios being 1.43 and 1.03 at day 10 and 15, respectively.

Cassinia aculeata was used in the germination experiment because it is abundant on roadsides and in the wetter parts near and within the studied areas. It is evident that the solution from the log shadow enhanced germination. Highly significant differences in the early days of germination demonstrate that *Cassinia aculeata* reacts positively to this environment.

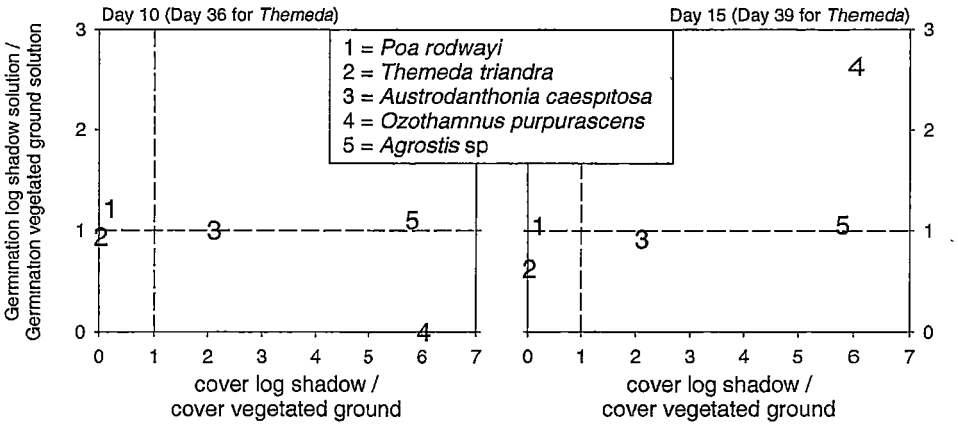

Figure 3.11. Relationship between germination in log shadow solution / germination in solution from well-vegetated ground and percent cover in log shadow / percent cover in well-vegetated ground.

The pattern showed at Day 15 (Figure 3.11) does not substantially change to the end of experiment. It is apparent that the nature of the soil solution does not affect the germination of most species. *Ozothamnus* is the major exception. *Ozothamnus* is a species that preferentially occurs in the log shadow and has enhanced germination in its soils. Whether this is a response to microbial antagonism in the soils of well-covered ground, or the chemical properties of the log shadow soil solution cannot be determined. *Themeda* neither successfully established in the log shadow nor successfully germinated in its soil solution. Again, the cause of this difference cannot be determined from the present data. The species that do not have a germination response to the difference in soil solutions are obviously preferentially distributed in one or other of these environments for other reasons. These may include relative competitive ability and relative drought resistance.

CHAPTER 4

Environmental and Floristic Patterns

Under The Canopy of *Eucalyptus globulus*

4.1 Introduction

The impacts on vegetation of variable environmental conditions under the canopy have been studied by various people. Reduced light availability is recognised by many as the primary cause for plants failing to colonize the soil under the canopy (Duggin and Gentle, 1998; Parendes and Jones, 2000). Colonization by plants is also believed to be hindered by the lack of some environmental resources such as available nutrients (Holmgren *et al.*, 2000; Maron and Jefferies, 1999) and water (Garcia-Fayos *et al.*, 2000; Yates *et al.*, 1996). The amount of water under the canopy may be reduced by root uptake (Morris *et al.*, 1998) in addition to the interception of precipitation by the canopy (Smith, 1974). In conditions in which nutrients and water are limited, Cruz (1997) believed that the shading effect of the canopy increases.

Litter accumulation may also be an important way in which a tree might modify its environment for its own benefit. Layers of resistant litter materials may provide more water by preventing excessive evaporation and colonization by other species (Clarke and Davison, 2001; Lloret, 1998). In fire-prone ecosystems, litter is a strong determinant of fire occurrence and intensity (Catchpole *et al.*, 2001), which will shape the floristic composition of post-fire

vegetation under the trees (Carry and Morrison, 1995), as well the plant community as a whole (Lindenmayer *et al.*, 2000).

Physical alteration of the soil caused by growing trees may involve stem and root expansion in combination with concentrated water flow from the stem. Common consequences are a lack of rooting medium, a rocky surface, and soil with relatively few fine particles. All these conditions may result in relative unsuitability of the subtratum for seedling emergence and survival (Lloret, 1998).

Species composition under the canopy of *Eucalyptus globulus* may vary in accordance with the stage of development of the tree (Scanlan and Burrows, 1990). When the trees are small, the biophysical impact on the surroundings could be expected to be minimal, with the understorey species composition more or less the same as the surrounding grassland (Loumeto & Huttel, 1997). The impacts are likely to become more and more apparent as the tree grows.

Despite the sparse canopy structure that allows a generous amount of light to penetrate to the ground underneath *Eucalyptus globulus,* that condition may not be an advantage for understorey colonizers if other environmental factors are limiting (Kirkpatrick, 1997; Yokozawa *et al.*, 1996). In this context, Cohn and Bradstock (2000) found an inconsistent effect of eucalypt canopy on the seedling survival of several understorey species.

The present chapter addresses two questions: How do environmental variables (soil total nitrogen, soil available phosphorus, soil organic matter content, and soil fraction composition) vary under the canopy of individuals of *Eucalyptus globulus* of various sizes? How does the floristic patterning of the understorey species relate to this variation?

4.2 Methods

Solitary trees were located. The criteria for a solitary tree were that (1) the distance to the nearest canopy of the neighbouring trees was at least twice the canopy diameter of the solitary tree, and (2) that distance did not fall on any part of a vehicle or walking track. Thirty trees, out of 50 that were located, were selected to represent a range of stem diameter classes. The diameter varied from 12.42 to 109.55 cm. The trees were then grouped into small (diameter <20cm, 7 trees), medium (diameter 20-40, 14 trees) and big (diameter >40, 9 trees). There were more medium sized trees than any other sizes. In diameter classes where more trees were available than needed, the choice was decided by use of random numbers. At the location of each tree, slope was measured and bulges in the ground that were obviously consequent upon root growth were counted. Two photographs at a 90 degree angle were taken for each tree in order to digitally calculate crown volume. The crown height was divided into ten sections. Each section was assumed to be cylindrical (Figure 4.1). The volume of each cylinder was determined from the

two photographs using the formula for elliptical cylinder. Crown volume was calculated by summing up the volumes of the ten cylinders.

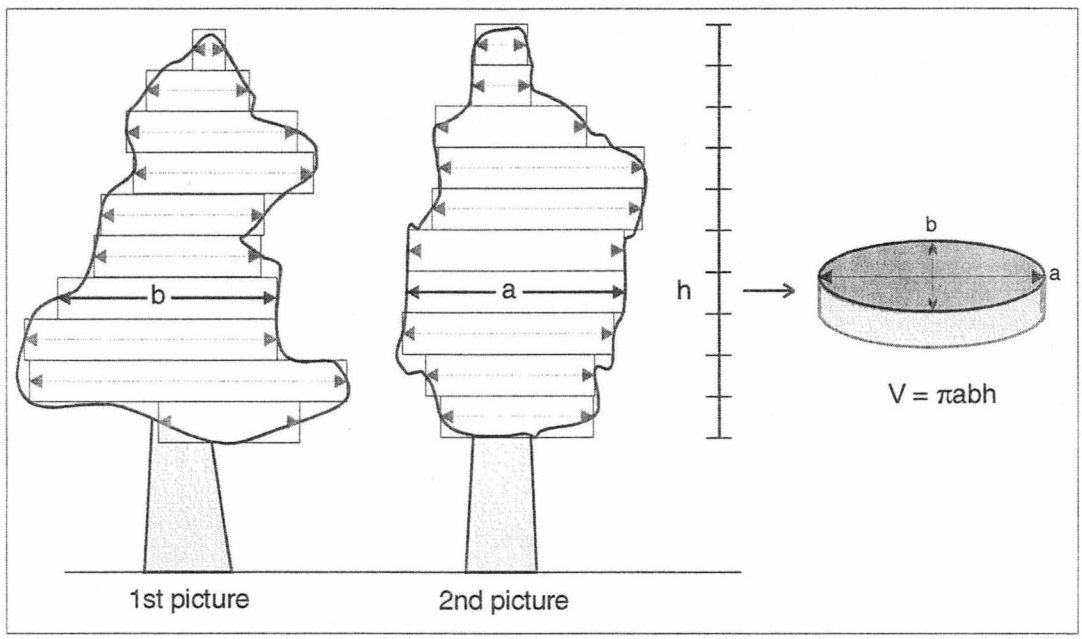

Figure 4.1. Diagram to calculate crown volumes.

Transects were laid from the tree base outward in four different directions according to slope orientation; the down, up, left and right side of the tree looking up-hill. This orientation was designed to capture the impact of stemflow, assuming that the majority of the water flows downhill as it arrives in the tree base, and the effect of the tree trunk on sediment movement.

Square plots (35 x 35 cm) were laid continuously along the transect from the base of the tree to half the distance of the canopy cover. For small trees, which had canopy edges of less than two metres, three plots were located for each

transect. All observable species in the sampling plots were recorded by percent cover, using estimation based on 100 squares within the quadrat frame.

Two soil cores (one from plot next to the trunk and another one from the outmost plot) were taken from each transect for 15 trees (out of the previously selected 30 trees) that were selected using random sampling stratified by tree size. Soil samples were immediately taken to the laboratory and air-dried. Total nitrogen, available phosphorus, organic matter content and soil fraction distribution were measured using the same methods as in Chapter 2.

The effects of slope direction, distance from the tree and tree size on soil nutrients, soil organic matter contents, soil fraction distribution, ground slope, and rock exposure were analysed with Analysis of Variance (ANOVA). If a significant difference was found, the Student-Newman-Keuls method of pairwise multiple comparison was employed.

The abundance data for species were used in an ordination of plots. The technique employed was multidimensional scaling (MDS) following the default options in DECODA (Minchin, 1990). A two-dimensional solution was suggested by the pattern of stress reduction. Community composition was related to stem diameter, crown volume, root extension, slope class, slope direction, and slope aspect by graphing the 95% confidence limits for groups in the ordination space.

4.3 Results

4.3.1 Soil Total Nitrogen

The average total nitrogen concentrations in the soil in the down and up side of the tree were 0.226% and 0.228%, respectively, while the left and right side of the tree contained higher nitrogen at 0.251% and 0.242%, respectively. The difference, however, was not significant ($F = 0.916$, $= 119$, $P = 0.4357$). Distance from the tree also did not significantly influence soil nitrogen content ($F = 0.570$, d.f. $= 119$, $P = 0.4517$). The average nitrogen contents in the soil next to the trunk was 0.241% and in the outer soil was 0.232%. The mean concentration of soil total nitrogen under the canopy was 0.24 ± 0.02 % (at a 99% confidence interval). Higher total nitrogen was observed in the soil under the medium-sized trees (0.265 %) than in the small and big trees (0.234% and 0.208%, respectively) (F-value = 7.673, d.f. = 119, and $P = <0.001$).

4.3.2 Soil Available Phosphorus

Soil available phosphorus did not vary by position in relation to the tree ($F = 0.342$, d.f. $= 119$, $P = 0.7953$). The down side soil contained 5.22 ppm of available phosphorus on average, the up, left and right side contained 4.68, 5.00 and 5.17 ppm, respectively. There was no significant difference between the soil located next to the tree base and the outer soil ($F = 1.69$, d.f. $= 119$, $P = 0.1955$). The mean of available phosphorus in the soil was 5.29 ppm next to the trunk and 4.75 ppm in the outer plots. The mean available phosphorus

under the canopy was 5.02 ± 0.54 ppm (at a 99% confidence interval). Soil available phosphorus did not significantly differ between trees of different sizes (F = 0.0625, d.f. = 119, P = 0.939). The means for available phosphorus for small, medium, and big trees were 5.01, 5.11, and 4.90 ppm, respectively.

4.3.3 Soil Organic Matter Content

The average organic matter content of soils located next to the tree base is 14.2%. The same amount is found in the soil more distant from the tree base (F = 0.00286, d.f. = 119, P = 0.9574). The average soil organic matter content in the down side of the tree base was 14.1%, the opposite up side soil contained 14.3%, while soil in the left and right sides of the tree contained 14.1% and 14.4%, respectively. The differences, however, are not statistically significant (F = 0.111, = 119, P = 0.9538).

Organic matter content in the soil near the tree base is affected by tree size (F = 3.40, d.f. = 59, P = 0.0401). The highest organic matter content is found next to the small trees (15.2%) and it is significantly different from that next to the big trees (13.0 %). Soil organic matter in the medium sized trees (14.5%) is not significantly different from the other two. Differences in soil organic matter contents between tree sizes weakened in the soil located more distant from the tree base (F = 0.0837, = 59, P = 0.9198) with average concentration is 14.4% for the small trees, 14.1% for the medium-sized trees and 14.2% for the big trees.

4.3.4 Soil texture

Soil fraction composition was not affected by slope direction or plot position, nor a combination of both. However, there were significant differences in soil particle size between tree sizes, both close and distant from the tree. The mean clay content in the soil next to the big trees is 27.9%, which is significantly higher ($F = 16.7$, d.f. = 59, $P = <0.001$) than next to the small and medium-sized trees (19.8% and 16.8%, respectively). The difference in clay contents is also apparent in the outer plots. Clay content in the soil under the big trees is significantly higher ($F = 8.99$, d.f. = 59, $P = <0.01$) than under the small and medium-sized trees. The average clay contents are 26.9%, 20.6%, and 18.6% for big, small and medium-sized trees, respectively. The difference is also apparent in the silt and sand fractions. Soil next to the trunk of small, mid-sized, and big trees contains 56.5, 59.0 and 49.9 % sand, respectively. The difference is highly significant ($F = 11.2$, d.f. = 59, $P = <0.0001$), the big trees being significantly different from the other two. Sand fractions in the outer plots also varied significantly with tree size ($F = 7.14$, d.f. = 59, $P = 0.0017$). Soil under the big trees contains 51.0% sand, which is significantly lower than both the small and medium-sized trees with 56.9% and 57.4% sand, respectively. Silt fractions were 24.2% in the soil next to the trunk of medium sized trees, which is significantly higher than the big trees with 22.2% silt ($F = 3.748$, d.f. = 59, $P = 0.030$). Soil in the base of the small trees contained 23.7% silt, which is statistically not different to the other two tree sizes. The difference in the outer plots is more robust ($F = 6.754$, d.f. = 59, $P = 0.002$)

where the silt fractions in medium-sized trees (24.1%) were higher than the small and big trees (22.6 and 22.1%, respectively).

4.3.5 Topography and Rock Cover

Among the 30 trees used for the other observations, only 23 trees were available for slope comparison because of missing records. Soils on the up side of the trunk were more level than soil on any other sides, with a 7.9° slope, which is significantly different to the up, left and right side slopes (15.4°, 15.7°, and 18.2°, respectively) ($F = 7.76$, d.f. = 91, $P = <0.001$). The ratio of down-side slope to the up side slope increased with tree size but this relationship was not statistically significant ($F = 1.77$, d.f. = 22, $P = 0.196$). The average slope ratios for the small, medium, and big trees were 2.4, 3.0, and 5.6, respectively.

There was no significant difference in rock exposure (in % ground cover) between soil on different sides of the trunk ($F = 0.38$, d.f. = 119, $P = 0.767$). The paired t-test analysis, however, revealed that rock exposure was higher in the down side of the trunk than the up side, averaging 22.1 % and 15.8 %, respectively ($N = 30$, t-value = 2.11, $P = 0.043$). Rock exposure significantly increased with tree size ($F = 119$, d.f. = 119, $P = 0.001$). Rock exposure was 4.4 % under the small tree compared to the 24.2 % and 27.5 % under the medium and big trees, respectively.

4.3.6 Species Patterns

Figure 4.2 shows that some understorey species preferentially occur close to tree trunks, while some others tend to occur away from the tree. Two species dominate the ground stratum at the study site, *Poa rodwayi* and *Themeda triandra* with 43.61% and 26.53% maximum leaf cover, respectively. *Poa rodwayi* preferentially grows under the canopy but not near the tree base and diminishes in cover with distance from the tree, while *Themeda triandra* gains both cover and frequency of occurrence with distance from the tree base (Figure 4.3).

Species in the next scale of dominance (1-10% maximum cover) that preferentially grow near *Eucalyptus globulus* tree bases are *Ranunculus lappaceus*, *Astroloma humifusum*, *Plantago lanceolata, Dichelachne rara*, and to a lesser extent *Plantago varia* and *Agrostis* spp.. *Austrodanthonia caespitosa* and *Schoenus apogon* seem to grow as well near the tree as away from the tree. The rest of the species in the list variably show gains in cover with distance from tree base.

Many species that were found in the low band of dominance (less than 1% maximum cover) show clear patterns of preference related to proximity to the tree trunk. Among the species that range between 0.25%-1% maximum cover, *Asperula* sp., *Ehrharta stipoides, Dichelachne* sp. and to a lesser extent *Lepidosperma gunnii* preferentially grow close to the tree. Some other species like *Oxalis perennans*, *Geranium* spp., *Gonocarpus tetragynus*, *Austrostipa*

semibarbata, *Acaena echinata, Carex breviculmis,* and, to a lesser extent, *Ehrharta distichophylla* occur relatively constantly with distance. *Wahlenbergia* sp. may also belong to this group. The rest of the species, namely *Arthropodium milleflorum*, and *Austrostipa aphylla* do not grow near the tree base.

Seedlings of three eucalypt species were found. *Eucalyptus globulus* seedlings grow near the tree while *E. pulchella* seedlings were found only in the 2^{nd}-5^{th} rings. *E. viminalis* was found at the greatest distance from the tree base.

In the lowest band of leaf cover (0.1 - <0.25% leaf cover), *Austrodanthonia* sp-b, *Kennedia prostrata*, *Opercularia varia* and *Cynoglossum suaveolens* show a preference for plots located next to the tree trunk. *Euchiton* sp., *Galium* spp. and, to some extent, *Anagallis arvensis* are found near the tree base but show an increase in cover with distance from the base. *Centaurium* sp., *Ozothamnus purpurescens* and *Olearia ramulosa* are not found at the tree base but their presence is limited to a close distance from the tree. *Hypericum gramineum* and *Leptorhynchos linearis* are found in plots near the tree as well as far from the tree. *Senecio glomeratus* does not grow near *E. globulus*.

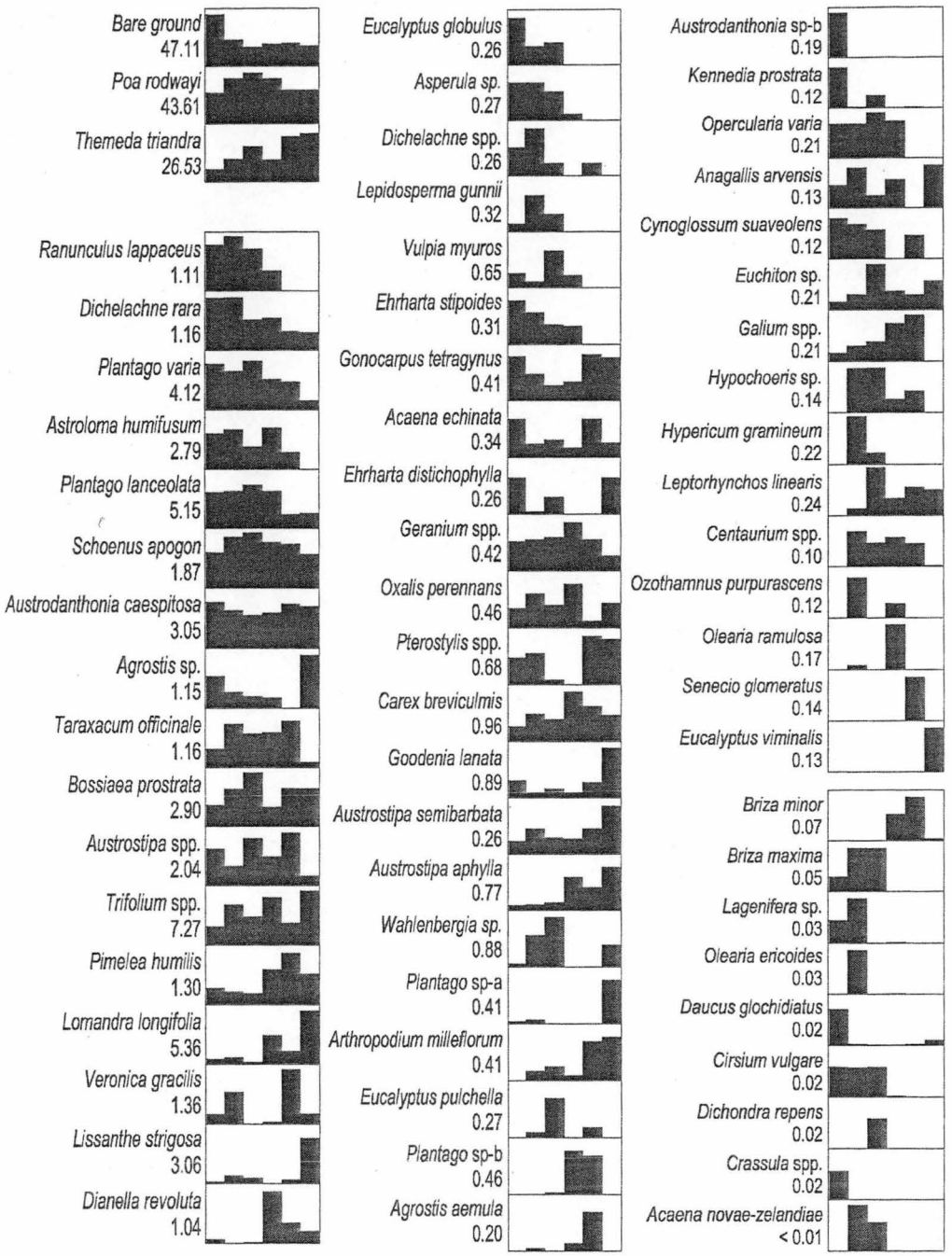

Figure 4.2. Cover (%) of the understorey species beneath the canopy of *Eucalyptus globulus*.

Note: Numbers indicate maximum percent cover. The vertical axis is cover expressed as a proportion of maximum cover. The horizontal axis is the distance from the tree trunk of the 35 x 35 cm^2 plots. Tree base is located on the left margin.

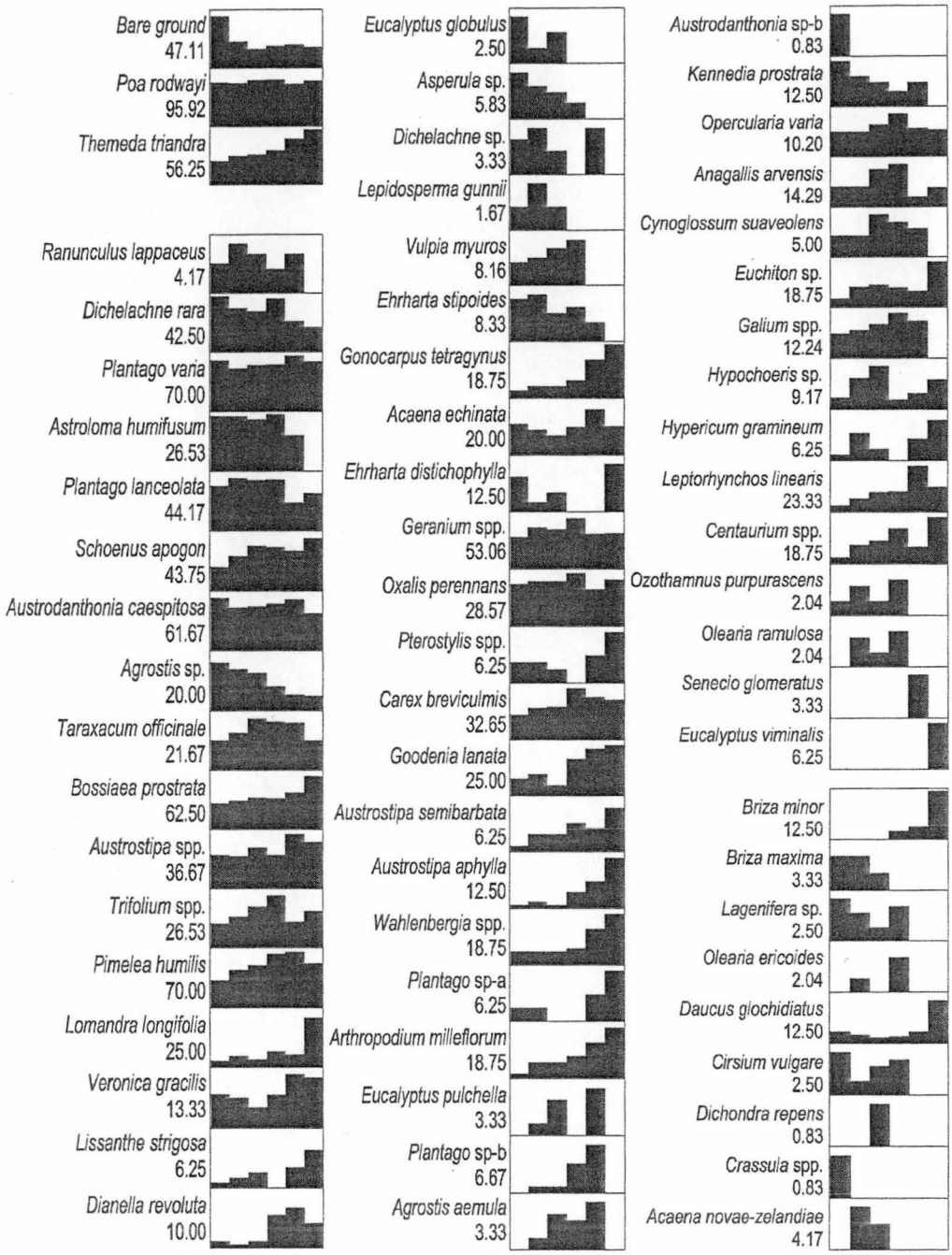

Figure 4.3. Frequency of occurrence (%) of the understorey species beneath the canopy of *Eucalyptus globulus*.
Note: Numbers indicate maximum percent cover. Ground cover % was used for the bare ground diagram. The vertical axis is frequency expressed as a proportion of maximum frequency. The horizontal axis is the distance from the tree trunk of the 35 x 35 cm^2 plots. Tree base is located on the left margin.

4.3.7 Floristic Composition

Tree diameter influences floristic composition close to the tree (Figure 4.4). For plots located immediate to the tree (R1), ordination scores were strongly separated by tree diameter class on the x-axis. The separation became less obvious when the plots were further from the tree base (R2). Plots most distant from the tree base (R3) did not show a distinct separation of the MDS values.

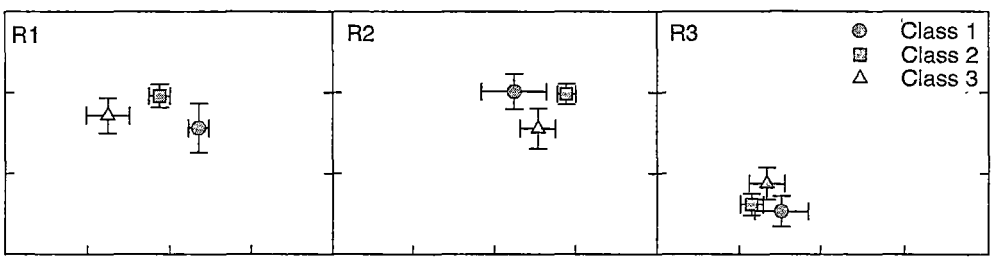

Figure 4.4. Distribution of tree diameter classes in ordination space. Note: Error bars represent 95% confidence limits. Class 1 < 20 cm, Class 2 = 20-40 cm, Class 3 = > 40 cm. R1 = on the tree base, R2 and R3 = 2nd and 3rd rings from the tree base, respectively.

Using the crown volume classes, the separation of MDS values is distinct only in the plots right next to the tree (Figure 4.5). Floristic characteristics under the trees with the lowest crown volumes seem to be distinct from the rest of the crown volume classes. Figure 4.5 also shows that among the plots of the tree bases (R1) there is an orderly sequence from the biggest crown class at the left of the X-axis to the smallest on the right. This suggests a strong influence of crown size on floristic pattern on the soil next to the tree trunk. The separation becomes less distinct among plots on the next circle (R2) from the tree base, although the smaller crowns seem to be slightly separated along the X-axis. In the outmost ring (R3), crown size becomes less important in determining

floristic composition of the understorey, as a separation of MDS values is not apparent.

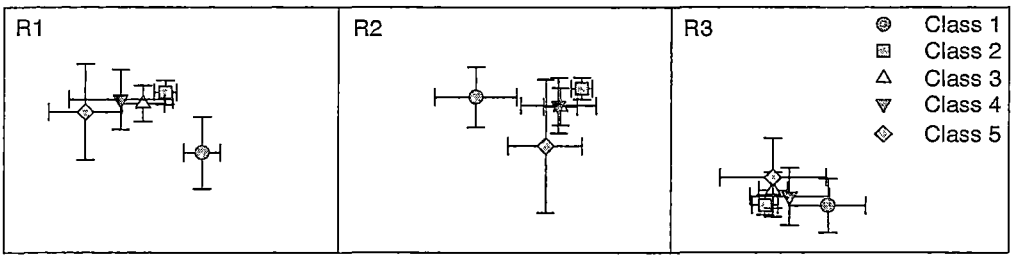

Figure 4.5. Distribution of crown volume classes in ordination space.
Note: Error bars represent 95% confidence limits. Class 1 = < 50 m^3, Class 2 = 50-150 m^3, Class 3 = > 150-350 m^3, Class 4 = > 350-1300 m^3, Class 5 = > 1300 m^3. R1 = on the tree base, R2 and R3 = 2nd and 3rd rings from the tree base, respectively.

The influence of root extension on understorey characteristics is also most apparent near the tree base (R1). Figure 4.6 shows that the separation of MDS values is reduced further away from the tree (R2 and R3).

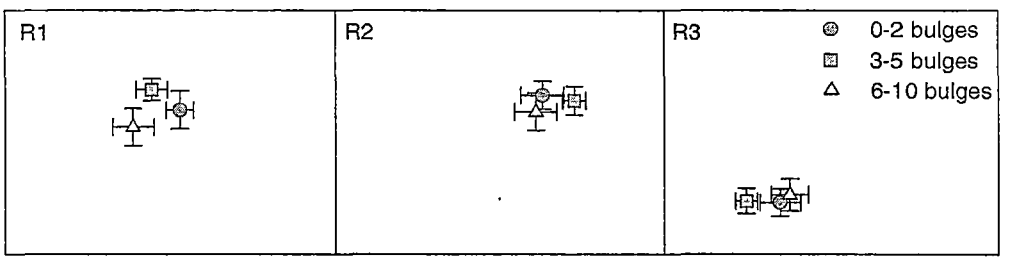

Figure 4.6. Distribution of root extension in ordination space.
Note: Error bars represent 95% confidence limits. R1 = on the tree base, R2 and R3 = 2nd and 3rd rings from the tree base, respectively.

Although not very strongly, there is separation of MDS values between plots with various positions relative to the tree (Figure 4.7). Plots positioned on the down side of the tree are located on the opposite side from the upslope plots in

the ordination space, but this is true only for plots in R1. The pattern disappears in the second and third rings.

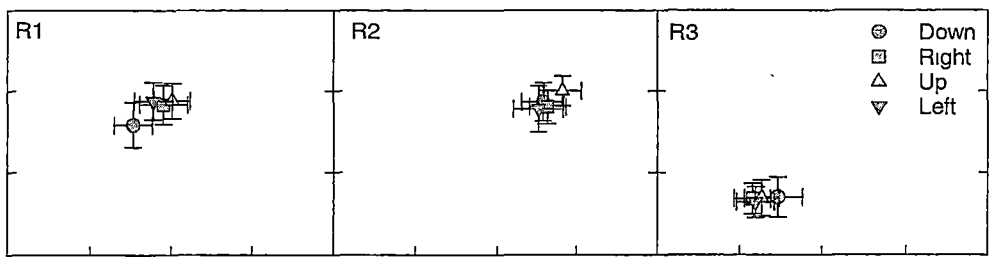

Figure 4.7. Distribution of slope directions in ordination space.
Note: Error bars represent 95% confidence limits. R1 = on the tree base, R2 and R3 = 2nd and 3rd rings from the tree base, respectively.

Slope only influences the floristic characteristics of vegetation that grows close to the tree base. Figure 4.8 shows a separation of MDS values only in plots near the tree base (R1 and to less extent R2).

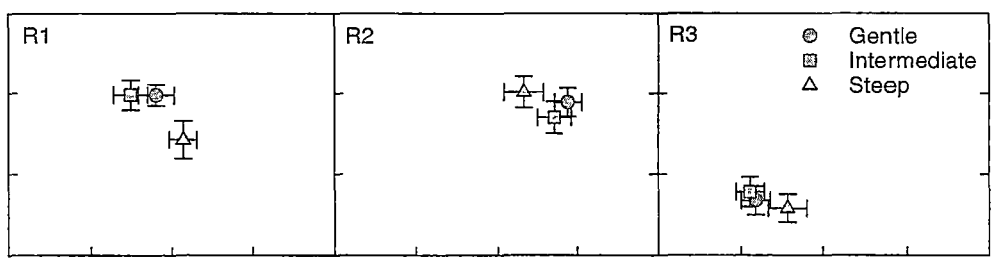

Figure 4.8. Distribution of slope classes in ordination space.
Note: Error bars represent 95% confidence limits. Groups are < 10, 10-20, and > 20 degrees for gentle, intermediate and steep slopes, respectively. R1 = on the tree base, R2 and R3 = 2nd and 3rd rings from the tree base, respectively.

Facing east may determine floristic composition of the understory species under *Eucalyptus globulus*. There is clear separation in MDS values of plots on east facing slopes located adjacent to tree trunk (R1 in Figure 4.9). Distinctiveness in floristic composition of the east facing slope is also apparent in the second ring (R2) and the order of separation seems to be consistent i.e.

east, south-east, north east and then either north-west or north facing slope. In the outmost ring (R3) it is the north and north-west facing slopes that make an apparent separation in ordination space. The other aspects (SE, E, NE) seem to cluster together although the east-facing slope is still located at the extreme end of the ordination space.

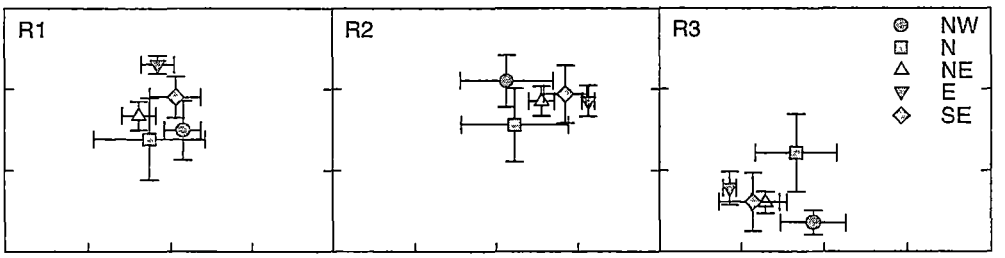

Figure 4.9. Distribution of slope-facing aspects in ordination space. Note: Error bars represent 95% confidence limits. R1 = on the tree base, R2 and R3 = 2nd and 3rd rings from the tree base, respectively.

4.4 Discussion

4.4.1 Environmental Variables

Evenly distributed conditions related to soil fertility (total nitrogen, available phosphorus and organic matter contents) were found under the tree canopy regardless of the distance from the trunk, slope, or position of the soil relative to the tree base. Previous work, reviewed by Kirkpatrick (1997), has shown that eucalypts may cause depletion of soil nutrients through root absorption and leaching by acidic stemflow. The results of the present study may suggest two things, (1) that these processes take place uniformly under the canopy and (2) that there is a high probability that water from stemflow is not a major

modifying force on soil nutrition in the environment. The results from the soil fraction analysis also did not differ with slope or position relative to the tree.

While soil available phosphorus was not influenced by the tree size, soil total nitrogen and organic matter contents were. The highest soil total nitrogen and organic matter contents were found beneath the medium-sized trees. It seemed that the tree might need to attain some age before it builds up nutrient pool under the canopy. Lesser nutrients in the soil under the small trees may be related to the a lesser amount of accumulated litterfall. Big trees, which are assumed to be survivors from the last (if not repeated) fires, might tend to store less nutrients under the canopy because of a slower decomposition rate as a result of possibly higher rate of interception of precipitation and great transpiration (Chapter 4).

The geomorphic alterations under the tree were, however, very profound. While there was evident that the soil in the down side from the trunk did not statistically differ from the left or right side of the tree, soil in the upper side was relatively level. It may indicate that the trunk is an effective sediment trapping mechanism and/or that erosion from stemflow works more forcefully in the left, right and down sides of the tree. Both explanations agree with the rock exposure data. Rock exposure was consistently higher in the down side of the tree compared to the up side of the tree.

4.4.2 Patterns of Species Distribution

Distance from the tree trunk has a strong effect on species presence and abundance. *Themeda triandra* and *Lomandra longifolia* may be typical of species that have a tendency to avoid soils near the tree trunk, in that they are relatively large and deep-rooted perennials. Species that are found relatively more abundantly near the tree trunk, such as *Dichelachne rara*, may take advantage of space left by the absence, or the reduced competitive ability, of more dominant species, such as *Themeda triandra* (Lavorel and Chesson, 1995).

Tree size only affects floristic composition in the plots that were located near to the trees. The variability in soil chemico-physical condition in the outer plots caused by differences in tree size did not cause variation in floristic composition. Floristic composition was found to be independent of tree size as the distance from the tree trunk increases. The same pattern of increasing independence with distance from the tree trunk occurs with variation in crown volume, root expansion, direction, and slope.

Variation in floristic composition in relation to aspect may be related to moisture and radiation conditions (Hogg and Kirkpatrick, 1974). Kirkpatrick and Nunez (1980) suggested that a xeric condition is associated with northwest and a mesic condition with southeast. At Conningham, the effect of aspect becomes more and more distinct as the distance from the tree trunk increases. Plots in the outer rings (R3 in Figure 4.9) display a floristic separation of the

north and northwest aspects. In the areas where the influence of tree is strongest (R1 in Figure 4.9), it is the more mesic aspects that are floristically separated from the other aspects.

The presence of *Eucalyptus globulus* only modifies floristic composition in a narrow area near the base of the tree, while water availability seems to influence floristic variability further from the trunk. Given that soil organic content, soil texture, nitrogen and phosphorus are statistically identical close to the tree and distant from the tree, the cause of the bare ground and floristic distinctiveness close to the tree must lie elsewhere. Possible explanations may lie in a high degree of eucalypt root occupancy of the soil and chemical inputs from stem flow.

CHAPTER 5

Differences in Nutrient Stores and Flows between *Eucalyptus globulus* Subcanopy and Intercanopy Areas

5.1 Introduction

Nutrient cycling is one of the major ecological processes that maintain ecosystems. The sustainability of this cycling is determined by the amount of nutrients stored in different components of the ecosystems and by the flux of the nutrients between these components. The majority of nutrient cycling studies deal with leaves and woody materials, which comprise the bulk of nutrient flux from plants to the soil (Burrows and Burrows, 1992; Grigg and Mulligan, 1999a; Hale and Pastor, 1998). Although the flux of nutrients through the fallen regenerative organs has not been totally ignored, it has been considered less important (Grigg and Mulligan, 1999b; Parrotta, 1999). Considering the highly concentrated nutrients in young plant organs (Bell and Williams, 1997), generalizations on nutrient flux through the study of leaf litterfall alone may be misleading. It may be necessary to study these young organs (buds or shoots) separately from leaves.

Grigg and Mulligan (1999a) showed that wet areas tend to produce more litterfall than dry areas. Studies of nutrient cycling in *Eucalyptus* dominated ecosystems have been concentrated in wet areas (see Keith, 1997), leaving a

gap to be filled by the present study. The role of animals in nutrient cycling in *Eucalyptus* forests is another gap the present chapter will address.

There are two important aspects of nutrient cycling that are widely examined: the amount of litterfall and the rate of decomposition. The amount of litterfall shows a broader picture of the biomass that is periodically returned to the soil by the vegetation. It expresses the pool of nutrients that might be made available when the litter breaks down into simpler structures or compounds. But knowing the size of the nutrient pool itself is not adequate. Resistant litter materials may reside on the ground for some time before they break down into simpler structures. Therefore, the rate of decomposition is vital in understanding nutrient cycling. It determines the amounts of nutrients that are released to the surroundings as decomposition progresses. Most studies in litter decomposition have been dedicated to leaves (Briones and Ineson, 1996; Pareira *et al*, 1998). However, different parts of plants may possess different resistance to decay. Generally, woody materials (e.g. bark and branch) decay slower then leaves and may accumulate on the ground (Brown *et al.* 1998).

Climatic conditions have a major influence on the amount of litterfall and the rate of decomposition. Burrows and Burrows (1992) showed a distinct seasonal nature of litterfall of various *Eucalyptus* species in woodland communities in central Queensland. Peak litterfall coincided with the period of increasing temperature from winter to summer and continued to autumn. Climatic conditions are also believed to strongly influence litter decomposition (Meentemeyer, 1978; Vitousek *et al.*, 1994). In grassy

woodland, climatic conditions under the canopy may vary greatly from those in the adjacent, open areas (Kirkpatrick, 1997).

The focus of the present chapter is on the difference between the subcanopy of the tree and the intercanopy area in: (1) the size of the nutrient pool of a range of litter components originating from *Eucalyptus globulus* and animals that consume the trees; (2) their decomposition rates; (3) the nutritional contribution of each litter component to nutrient cycling processes; (4) the seasonality of the above.

5.2 Methods

5.2.1 Litterfall

All thirty trees selected for studies in Chapter 4 were used for litter collections. Plastic litter traps with 938 cm^2 area and 6 cm depth were used to collect litterfall. A 5-mm hole covered with nylon screen (1-mm mesh) was made to allow drainage from the trap. The traps were set level on wooden pegs. Litter traps were set in the down, up, left and right sides of each tree, one under the canopy and one in the open at twice the distance from the trunk to the canopy edge. There were eight traps for each tree giving 240 traps in total. Litter traps were emptied at fortnightly intervals and following rain events. All litter was oven dried (80 ^{O}C, 48 h), sorted into leaves, buds (containing young shoots and flowers), fruit (capsules), bark and branches, and then weighed. Data are presented as g/m^2. Plant litter from species other than *Eucalyptus globulus* was

discarded. Animal droppings were also collected and sorted. The oven dried litter was bulked every four weeks and then ground up for nutrient analysis. Total nitrogen and phosphorus were measured using methods described by Allen (1974).

5.2.2 Throughfall and Stemflow

Throughfall was collected in 4750 cm^2 area (190 x 25 cm) of galvanized, V-shaped collectors that drained into 15-liter plastic containers. The collectors were set under the trees. Stemflow was collected using elastic tubes that were belted around sampling trees and drained into 5- or 15-litter containers, depending on the size of the trees. Four and seven trees representing various tree classes were randomly selected for throughfall and stemflow measurements, respectively. Local precipitation was measured using a rain gauge that was set up in the open according to the general requirements for a rain station. Water containers and rain gauge were emptied the following morning after every rain event. To reduce temporal variability, water samples for nutrient analysis were taken at the same time for all trees, that was when the tree with the smallest amount of moisture had enough water for the analysis. Nitrogen and phosphorus contents in the water were analyzed according to methods decribed by Rayment and Higginson (1992).

To make a common comparison through various ranges of rainfall, stemflow (in mL) was first transformed to mm unit by the factor of basal area. It then

was converted to a Relative Stemflow (%), that is a proportion of stemflow relative to the total rainfall of the simultaneous rain event. It was expected that the Relative Stemflow would exceed 100% since the conversion was made using basal area, but the rain catchment area could be as big as the canopy area.

5.2.3 Decay Rates

Decay rates of *Eucalyptus globulus* leaves, barks and branch, and possum droppings were studied using 2-mm nylon mesh bags (15 x 15 cm). Litter materials were collected on site from freshly fallen litter two weeks before being placed in the ground. *Eucalyptus* leaves, barks and branch were air dried and cut to fit the bags, weighed and placed into the mesh bags. Possum droppings were air dried and put straight to the bag. About the same amount of material was oven dried to obtained initial water and nutrient contents. Decomposition prior to bagging and air-drying is negligible. The following formula was used to obtain the initial water content:

$$Wi = 1 - (Lo/Lf)$$

where Wi is initial water content, Lo is litter oven dried weight and Lf is litter fresh weight. The initial litter biomass at setting (Li) is obtained by the following formula:

$$Li = Lf(1-Wi)$$

where Lf is litter fresh weight and Wi is the initial water content.

Dropping and leaf mesh bags were placed in the field in November 1998 (30 bags each) and the following February (20 bags), May (20 bags), and August (20 bags), one half under the canopy and the other half in the open. The trees were randomly selected among the 30 trees used for the litterfall observation. Five samples of each of the two litter materials were randomly retrieved from under the canopy and in the open at 6 and 18 weeks following the placement to study the seasonal variability in decomposition. The extra 10 bags for November placement were retrieved at the 54^{th} weeks and were used to construct decay curves both under the canopy and in the open. Ten mesh bags each for bark and branch litter were also placed in November again one half under the canopy and the other half in the open. They were retrieved at once at 52 weeks after the placement. In every excavation, five bags were retrieved from under the canopy and five from the open for each litter type. The retrieved bags were cleaned from soil and debris using a soft paint brush and emptied. The decomposed litter was oven dried and weighed. Nitrogen and phosphorus contents were then obtained.

The litter remaining weight (*Lr*) is obtained using the following formula.

$$Lr = Ld / Li * 100\ \%$$

Where *Ld* is the oven-dried weight of the decomposed litter and *Li* is the litter initial weight.

5.2.4 Statistical Analysis

Three variables were tested and compared in this study: decay rates obtained by curve fitting procedure; actual litterfall at various times of the year; the accumulated litterfall at the end of the year. The half life of each litter type is presented for practical comparison.

Rates of decomposition were obtained by curve-fitting procedures. This was by means of nonlinear regression analysis using an iterative process that stops when the best fit equation converged to the negative exponential decay model below,

$$Yt = Yo^{-kt}$$

where Yt is weight at time t, Yo is the initial weight, and k is decay rate. The model was ln-transformed before the procedures were employed. The model was derived from Olson (1963).

To calculate the half life, that is time needed when half of the initial biomass has decayed (or $Yt = 0.5\ Yo$), the following equation was derived

$$\ln(Yt) = \ln(Yo) - kt \text{ or}$$

$$-kt = \ln(Yt) - \ln(Yo) \text{ or}$$

$$-kt = \ln(Yt/Yo)$$

and by substituting Yt with $0.5Yo$,

$$-kt = \ln(0.5) \text{ or}$$

$$t_{½} = 0.693/k$$

Analysis of covariance of decomposed litter materials was conducted to examine the difference between decay curves under the canopy and in the open. The analysis was conducted on ln-transformed of the remaining weight by means of SAS' General Linear Models Procedure with time (t) as a covariant (SAS Institute, 1988). Leaf litter and possum droppings buried on November 1999 were used for this purpose with decomposition time ranged between 0.12 (6), 0.35 (18), and 1.04 years (54 weeks).

One-way analyses of variance (ANOVA) were used to make comparisons between litterfall under the canopy and in the open and litterfall variability across seasons. If a significant difference was detected, the Student-Newman-Keuls Method of Multiple Comparison was employed.

5.3 Results

5.3.1 Seasonal Patterns of Litterfall

5.3.1.1 *Eucalyptus globulus* Leaves

Litterfall of *Eucalyptus globulus* leaves showed a strong pattern of a steady increase through summer followed by a sharp drop in the beginning of autumn and then constantcy until the start of summer (Figure 5.1). Variability of monthly leaf litterfall is significant both under the canopy and in the open ($F = 25.6$, d.f. = 389, $P < 0.0001$). *E. globulus* leaf litterfall peaked in the 1st March collection at 18.83 and 17.03 g/m^2 for under the canopy and in the open. These

rates are significantly higher than the other months, with the exception of February. There is a small increase at the end of spring (8 November), followed by a decline in December.

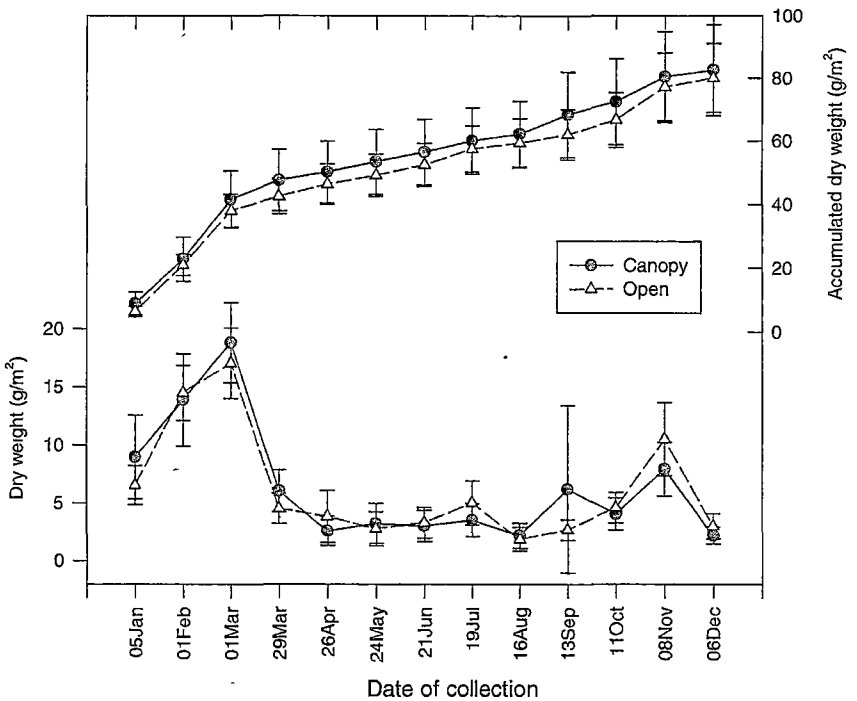

Figure 5.1. Monthly and accumulated litterfall of *Eucalyptus globulus* leaves.
Note: Vertical bars represent 95% Confidence Intervals.

There is a strong similarity in the amount and temporal patterns of *E. globulus* leaf litterfall between the under canopy traps and those in the open (Figure 5.1). The accumulated leaf litterfall under the canopy and in the open was not significantly different by the end of the year ($F = 0.0750$, d.f. = 59, $P = 0.7852$). Total annual leaf litterfall under the canopy of *Eucalyptus globulus* is 82.57 g/m2, compared to 80.13 g/m2 of leaf litterfall in the open.

5.3.1.2 *Eucalyptus globulus* Buds and Fruit

Bud and flower litterfall of *Eucalyptus globulus* increased from January to July followed by a sharp drop to a minimum on August. This pattern is true for litterfall both under the canopy and in the open (Figure 5.2). Litterfall under the canopy continues to increase to a highest point on December (4.03 g/m^2) while the litterfall in the open reaches its maximum on November (1.98 g/m^2). Differences in monthly litterfall were highly significant both under the canopy ($F = 2.76$, d.f. = 389, $P = 0.0013$) and in the open ($F = 3.44$, d.f. = 389, $P < 0.0001$). The lowest litterfall occurred in August (0.72 and 0.19 gr/m^2, for under canopy and in open respectively). The difference in accumulated litterfall between the traps under the canopy and in open becomes more and more distinct with time (Figure 5.2). The annual litterfall under the canopy of *Eucalyptus globulus* is 28.6 g/m^2, which is significantly higher than in the open with 14.3 g/m^2 ($F = 9.51$, d.f. = 59, $P = 0.003$).

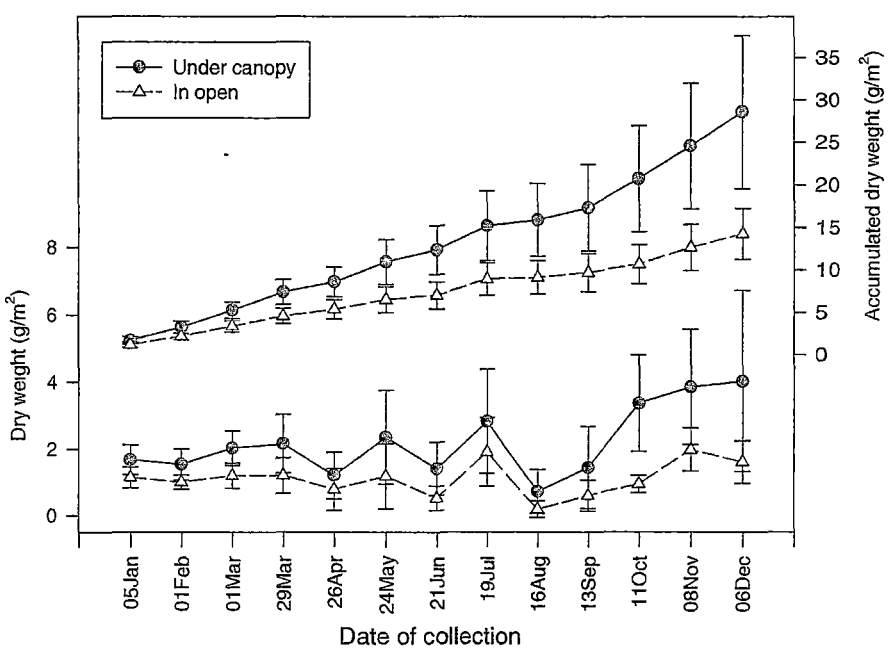

Figure 5.2. Monthly and accumulated litterfall of *Eucalyptus globulus* buds and flowers.
Note: Vertical bars represent 95% Confidence Interval.

The fruit litterfall of *Eucalyptus globulus* was more concentrated under the canopy than in the open (Figure 5.3). The monthly fruit litterfall under the canopy varies significantly ($F = 1.843$, d.f. = 389, $P = 0.040$). Litterfall peaks in January (0.94 g/m^2) and levels off to the end of March, then declines afterwards. Annual fruit litterfall is 4.40 g/m^2 under the canopy and 0.27 g/m^2 in the open. The difference is statistically significant ($F = 33.386$, d.f. = 58, $P < 0.001$).

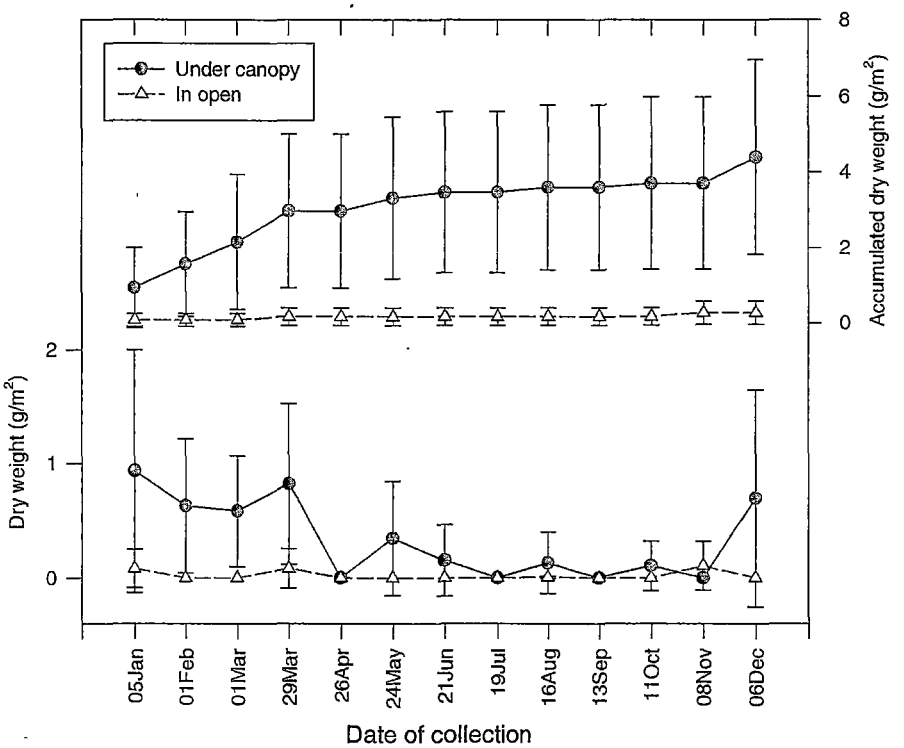

Figure 5.3. Monthly and accumulated litterfall of *Eucalyptus globulus* fruit.
Note: Vertical bars represent 95% Confidence Interval

5.3.1.3 *Eucalyptus globulus* Bark and Branches

Bark litterfall makes the biggest contribution to the total *E. globulus* litterfall. The annual litterfall of bark is 102.70 g/m^2 under the canopy, which is significantly higher than the 27.12 g/m^2 in open ($F = 35.7$, d.f. = 59, $P < 0.0001$). Bark litterfall showed a slightly different pattern to leaf litterfall. Figure 5.4 shows that bark litterfall peaked on May (17.32 g/m^2 under the canopy) or occurred more often during April through June and dropped to the lowest point on August (1.60 g/m^2 under the canopy and 0.46 g/m^2 in the opening). Bark litterfall under the canopy increases to another peak on November. The open area bark litterfall, however, stayed relatively constant to December. Figure 5.4 shows that monthly litterfall is higher under the canopy except for February. However, statistically significant differences between under the canopy and in the open occur only on November, December and March.

The Difference between the accumulated litterfall under the canopy and in the open becomes significant at the end of March and the disparity becomes more significant with time (Figure 5.4).

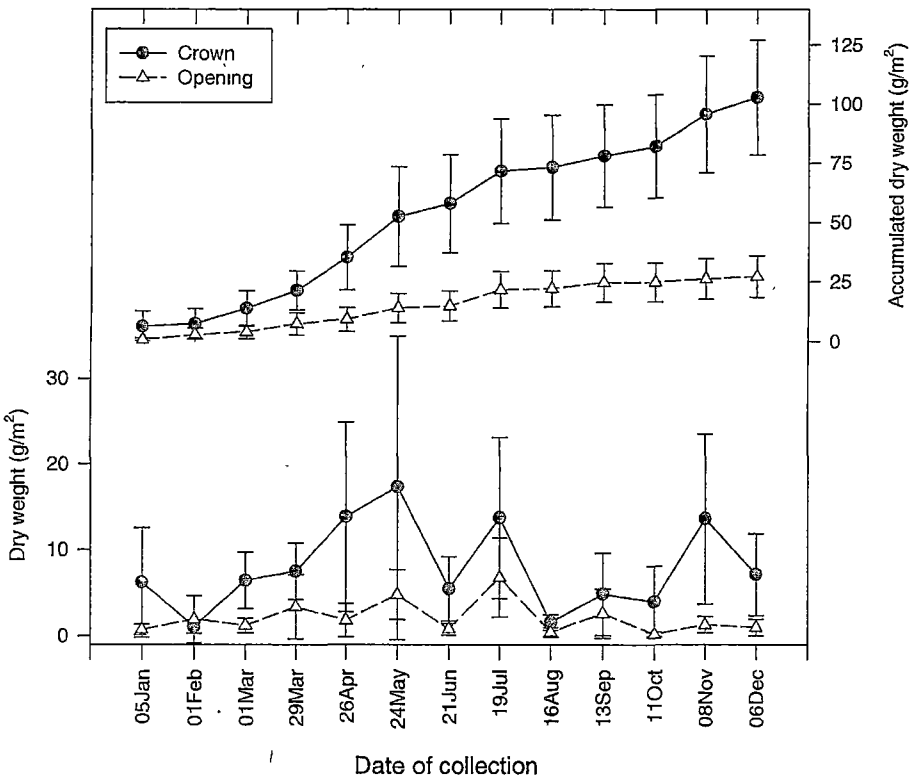

Figure 5.4. Monthly and accumulated litterfall of *Eucalyptus globulus* bark.
Note: Vertical bars represent 95% Confidence Interval

Branch litterfall of *Eucalyptus globulus* is relatively even through the year, and no seasonal pattern is observed (Figure 5.5). Date of collection did not significantly alter branch litterfall either under the canopy or in the open. Figure 5.5 shows that branch litterfall under the canopy was higher than in the open with exception of March. In late March, branch litterfall in the opening jumped slightly higher (4.91 g/m^2) than the litterfall under the canopy (3.57 g/m^2). ANOVA shows that the annual litterfall under the canopy (35.1 g/m^2) is significantly higher than in the open (15.2 g/m^2) with $P = 0.0286$ ($F = 5.04$, d.f. = 59).

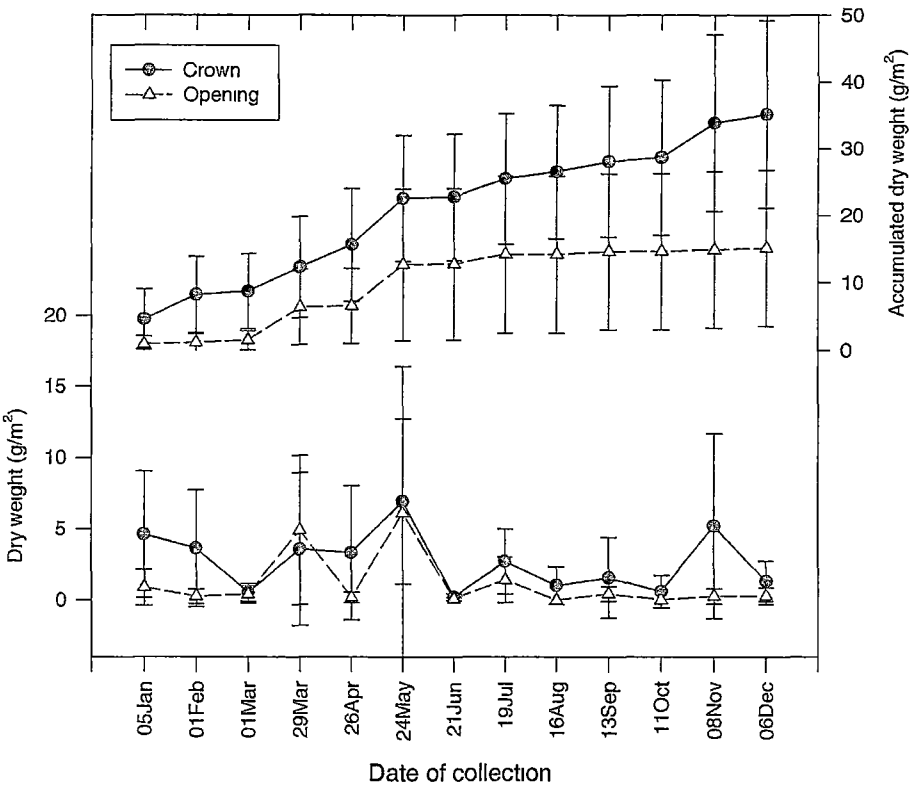

Figure 5.5. Monthly and accumulated litterfall of *Eucalyptus globulus* branches.
Note: Vertical bars represent 95% Confidence Interval.

5.3.1.4 Animal Droppings

Seasonal patterns and the annual total of animal litter are largely determined by possum droppings. Under the canopy where the animal litter is most concentrated, droppings of all other animals combined together (0.216 g/m^2) contribute only 2.5 % to the total annual animal litter (8.70 g/m^2). Annual litterfall of possum droppings under the canopy is 8.48 g/m^2, while it is only 0.76 g/m^2 collected in the litter traps in open space. The difference is highly significant (F = 2.04, d.f. = 59, P = 0.0092). Possum litter did not show a significant variation through the year whether it was under the canopy or in

the open (Figure 5.6). The maximum possum droppings in the open occurred in October, at which time the droppings under the canopy were at their minimum.

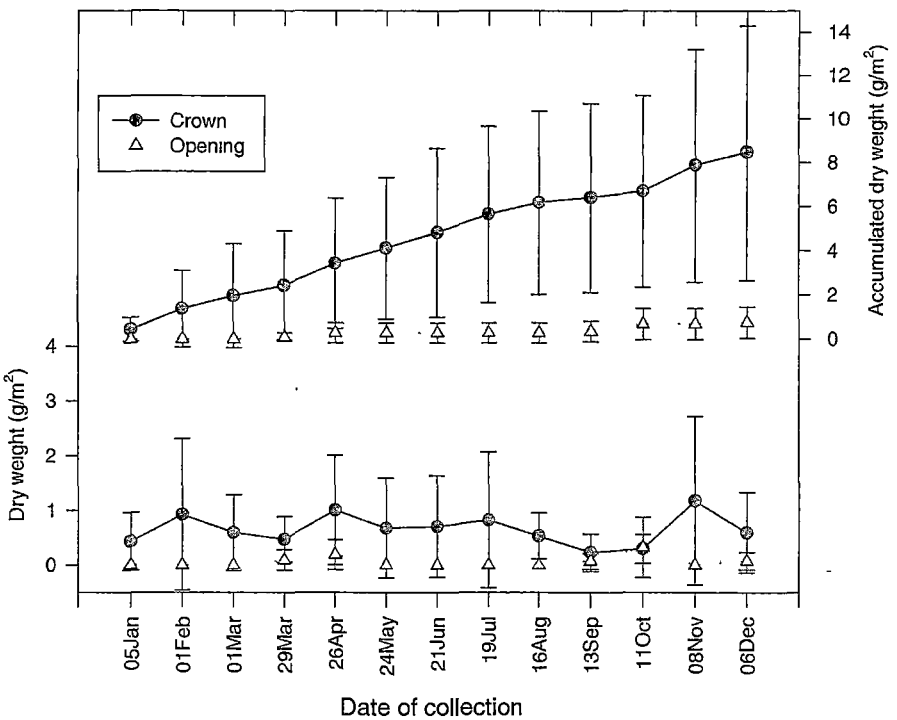

Figure 5.6. Monthly and accumulated possum droppings.
Note: Vertical bars represent 95% Confidence Interval.

Bird droppings were very small with a maximum monthly fall of 0.008 g/m^2 in August under the canopy. Differences between monthly droppings are not significant. Bird droppings were found in two time periods, between late summer to early autumn (early March to late April) during which time the traps in the open collected more droppings, and between mid-winter to early summer (mid August to early December) during which time the traps under the canopy collected more droppings. The differences, however, were not

significant. Annual litterfall from bird dropping under the canopy is 0.0157 g/m^2, which is statistically not different to the 0.013 g/m^2 in the open.

Wallaby droppings were found between late March to May in the open and only in July under the canopy. Annual litterfall from wallaby droppings is 0.056 g/m^2 under the crown and 0.27 g/m^2 in open. The difference, however, is not statistically significant. Rabbit droppings were found mainly during summer. The annual total is 0.15 g/m^2 under the canopy and 0.13 g/m^2 in open. The maximum monthly droppings under the canopy occurred in January (0.078 g/m^2) and, in the open, in early March (0.057 g/m^2).

5.3.2 Seasonal Variations in Nutrient Concentrations

5.3.2.1 *Eucalyptus globulus* Leaves

Nitrogen content in leaf litter showed a distinct seasonal pattern (Figure 5.7). Leaf litter nitrogen variably, but constantly, increased from a minimum in February (0.43%) January to reach a peak in July (0.76%). The variability in monthly nitrogen concentrations throughout the year is highly significant ($F = 12.2$, d.f. = 38, $P < 0.0001$). *Eucalyptus globulus* leaf litter tends to have less nitrogen during summer.

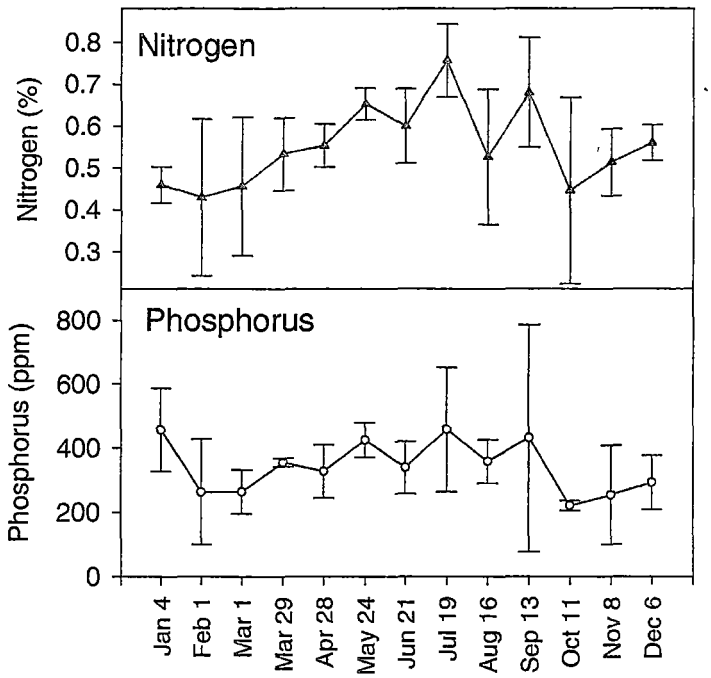

Figure 5.7. Nitrogen and phosphorus contents in *Eucalyptus globulus* leaf litter.
Note: Vertical bars represent 95% confidence intervals.

Phosphorus content in *Eucalyptus globulus* leaf litter did not show a strong seasonal variability (Figure 5.7). Analysis of variance of monthly phosphorus concentration in the leaves, however, showed highly significant differences ($F = 5.99$, d.f. = 38, $P < 0.0001$). Leaf phosphorus concentration peaked in January (457.3 ppm) but then dropped to almost the lowest point in February (264.0 ppm). It then variably increased to another peak on July (457.3 ppm) and then declined to its lowest point in October (221.0 ppm).

5.3.2.2 *Eucalyptus globulus* Buds

Flower buds and young twigs were grouped as buds. The gap in the nitrogen data in Figure 5.8 was because the samples were lost before the nitrogen content was analyzed. *Eucalyptus globulus* bud litter nutrients showed distinct seasonal patterns (Figure 5.8). Analysis of variance showed highly significant monthly differences for nitrogen ($F = 12.6$, d.f. = 35, $P < 0.0001$) and phosphorus ($F = 11.6$, d.f. = 38, $P < 0.0001$) concentrations in bud litter. Bud nitrogen concentration peaked on early March (1.00%) and significantly declined afterwards to reach a minimum on May (0.46%). It was relatively constant through the rest of the year. Phosphorus content peaked also in early March (747 ppm). The minimum phosphorus concentration is found in June (608 ppm). In the first half of the year, the pattern of phosphorus concentration resembled that of nitrogen.

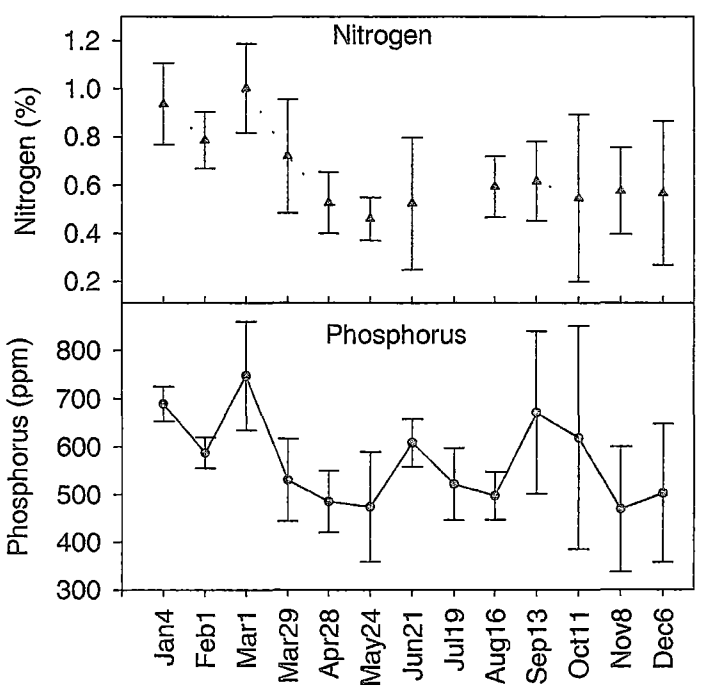

Figure 5.8. Nitrogen and phosphorus contents in *Eucalyptus globulus* bud litter.
Note: Vertical bars represent 95% confidence intervals.

5.3.2.3 *Eucalyptus globulus* Woody Parts

Nutrient contents of woody litter showed a distinct seasonal pattern that almost resembled that of bud litter nutrients. Analysis of variance shows a significant difference in monthly contents of nitrogen ($F = 8.08$, d.f. = 35, $P < 0.0001$) and phosphorus ($F = 23.9$, d.f. = 37, $P > 0.0001$) in *Eucalyptus globulus* woody material. Figure 5.10 shows that woody litter nitrogen and phosphorus peaked in February (0.39% and 263 ppm, respectively) and variably declined to minima in May (0.17% and 89 ppm, respectively). Both nitrogen and phosphorus concentrations climbed up to another peak on October and both had a low on September. The decline in phosphorus is highly significant (Figure 5.9). Unlike the nutrient contents of leaf and bud litter, both nitrogen and phosphorus concentrations in the January woody litter were much lower compared to February litter.

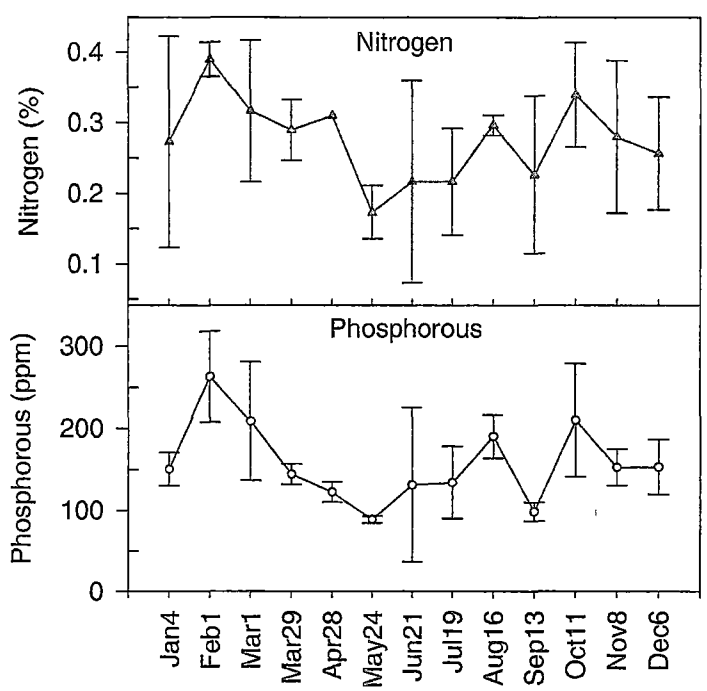

Figure 5.9. Nitrogen and phosphorus contents in woody litter of *Eucalyptus globulus*.
Note: Vertical bars represent 95% confidence intervals.

5.3.2.4 Animal Droppings

Data variability in possum dropping nitrogen content was exceptionally large in April. This lessened the magnitude of disparity of nitrogen concentration from month to month (Figure 5.10). Nevertheless, analysis of variance showed that differences in monthly nitrogen were highly significant (F = 2.87, d.f. = 42, P = 0.0094). Figure 5.10 shows that after remaining in a plateau during the first five months of the year, nitrogen concentration in possum dropping increased to a peak (2.29%) in June and then declined to a minimum (1.53%) in September. It rose to a maximum (2.33%) on October and then steadily declined in the following months.

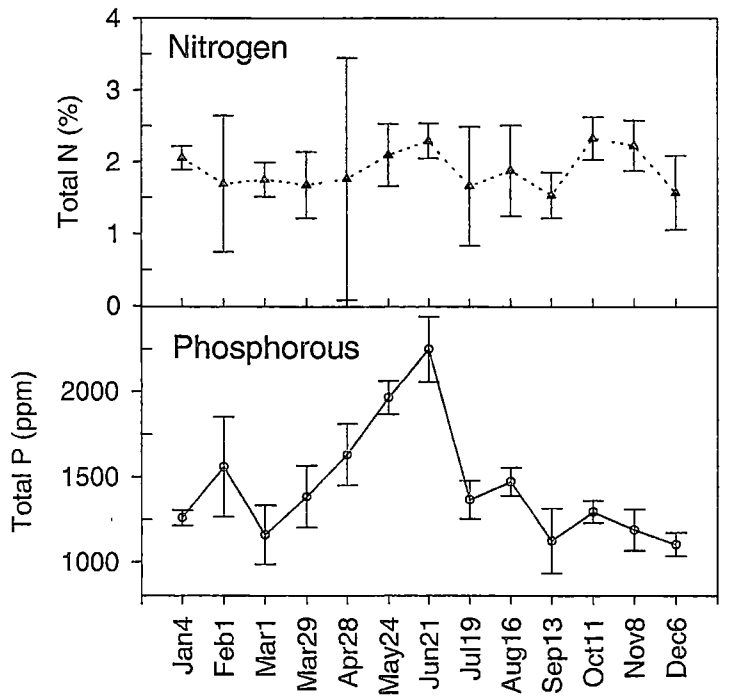

Figure 5.10. Nitrogen and phosphorus contents in possum droppings.
Note: Vertical bars represent 95% confidence intervals.

Phosphorus content in possum dropping shows a completely different pattern. Analysis of variance showed a highly significant difference in phosphorus concentration in possum dropping collected in various months of the year ($F = 103.8$ d.f. = 42 $P < 0.0001$). Figure 5.10 shows a marked increase of phosphorus contents from the beginning of the year to reach a maximum (2248 ppm) in June. It then sharply declined to reach a minimum (1124 ppm) in September and leveled out in the following months. What makes the possum dropping phosphorus pattern different to the other litter materials is that it has only one maximum and all the others had two.

5.3.3 Precipitation

5.3.3.1 Stemflow

Relative Stemflow varies significantly with tree size ($F = 13.9$, d.f. = 116, $P < 0.0001$). Figure 5.11 shows that higher relative stemflows were found in trees of moderate sizes. The smallest tree (basal area 168 cm^2) had the lowest stemflow and was significantly different from trees of any other sizes. The stemflow constantly increased as the tree size increased and peaked (1124%) at a moderate basal area of 1583 cm^2 although it was not significantly different to the other smaller, mid-sized trees (basal area 1264 and 845 cm^2). As the tree size increased (basal area 2194 cm^2) stemflow dropped significantly to about 319% and further to 176% of total rainfall in the biggest tree (basal area of 9422 cm^2).

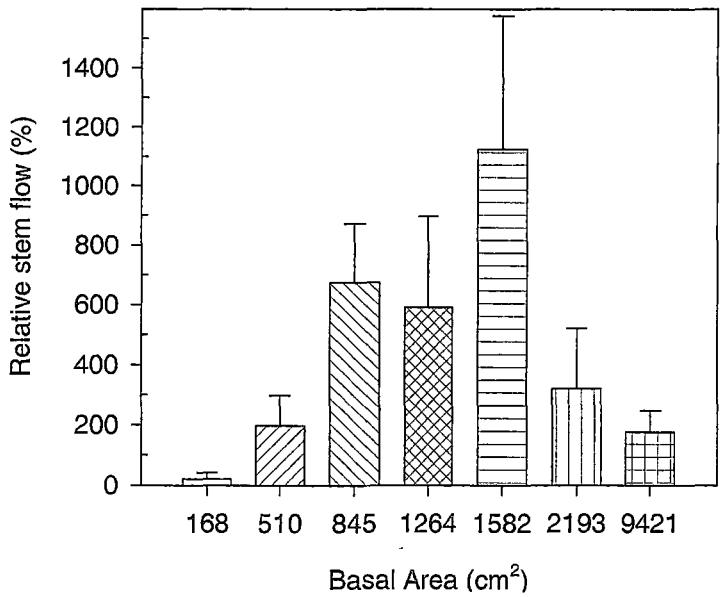

Figure 5.11. Relative stemflow with basal area of *Eucalyptus globulus*.
Note: Vertical bars represent 95% confidence intervals.

5.3.3.2 Throughfall

Throughfall was converted to a mm unit by the factor of the area of the trough (4750 cm^2). *Relative Throughfall* was then calculated as a percentage of throughfall deposition relative to the total rainfall of the simultaneous rain event.

Relative throughfall was also significantly affected by tree size ($F = 29.4$, d.f. $= 68$, $P < 0.0001$). The smallest tree (basal area =510 cm^2) let only 10.19 % of total rainfall through the canopy (Figure 5.12). It is a small figure in comparison to the relative throughfall of the next bigger tree with 1583 cm^2 basal area, which has 11.12% relative throughfall. The difference, however, is

not statistically significant. As with relative stemflow, relative throughfall seemed to peak at this moderate tree size. Once the tree size increased the mean relative throughfall dropped to 10% and significantly decreased even more to only about 5% for the biggest tree available in this study, which has a basal area of 9421 cm^2.

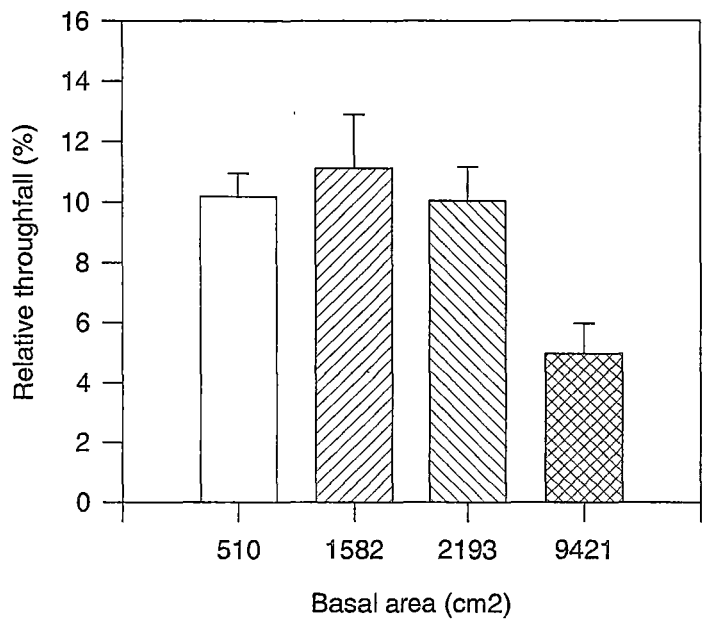

Figure 5.12. Throughfall with basal area of *Eucalyptus globulus*.
Note: Vertical bars represent 95% confidence intervals.

5.3.3.3 Nutrient Levels

The means of total nitrogen content in stemflow is 0.71 ppm with data range between 0.20 -1.49 ppm. Nitrogen content in stemflow poorly correlated to tree size (N = 12, R^2 = 0.1068). Phosphorus content in stemflow is either 0.02, 0.01 or < 0.01 ppm, too low to analyze. Total nitrogen content in the throughfall varies between 0.27-0.46 ppm, with an average of 0.36 ppm. It does not correlate to tree size (N = 5, R^2 = 0.0048). Phosphorus content was always less than 0.01 ppm.

5.3.4 Litter Decomposition

5.3.4.1 Curve Fitting Procedures for *Eucalyptus globulus* Leaves

Curve fitting procedures confirmed that the decomposition of *Eucalyptus globulus* leaves, both in the open and under the canopy, followed the negative exponential decay model (Table 5.1). There is great confidence in the model with adjusted R^2 equal to 0.905 for decomposition in the open and 0.843 under the canopy ($F = 162.8$, d.f. = 17, $P < 0.0001$ for open mesh bags and $F = 103.1$, d.f. = 19, $P < 0.0001$ for mesh bags under the canopy). Analysis of covariance suggested that *Eucalyptus globulus* leaves incubated under the canopy decayed significantly slower than in the open ($F = 115.95$, d.f. = 37, $P = 0.0001$, $R^2 = 0.87$). The decay rates (k) are 0.414/year under the canopy and 0.294/year in the open.

Table 5.1. Rate of decomposition (k), adjusted R^2, degree of freedom, F-values and P-values of curve-fitting procedure for *Eucalyptus globulus* leaf decomposition

Location	k	Adj. R^2	d.f.	F	P
Open	0.294	0.905	17	162.8	<0.0001
Canopy	0.414	0.843	19	103.1	<0.0001

Significant difference in weight loss was not detected until 54 weeks after burial (Figure 5.13). Leaf litter under the canopy would decay to half of the initial weight in 2.4 years (or 122 weeks), but leaf litter in the open would take only 1.7 years (87 weeks).

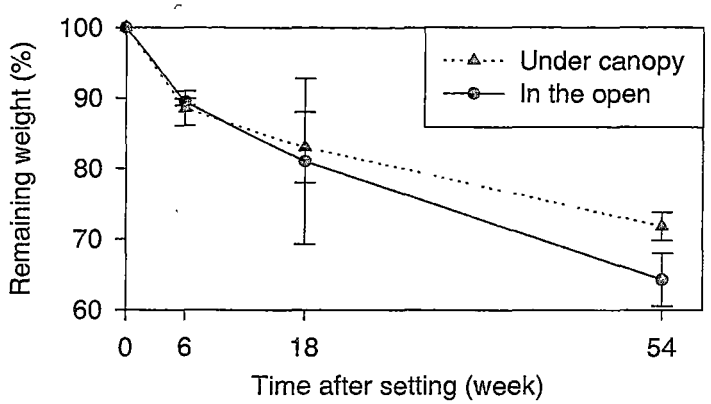

Figure 5.13. Comparison of *Eucalyptus globulus* leaf litter weight loss (% of initial weight) under the canopy and in the open.
Note: Vertical bars represent 95% confidence intervals.

5.3.4.2 Curve Fitting Procedures for Possum Dropping

The decomposition of possum dropping both under canopy an in the open followed the negative exponential decay model. Curve fitting procedures produce adjusted $R^2 = 0.947$ for litter in open and 0.893 under the canopy (Table 5.2). Analysis of covariance showed that the decay rate (k) in the opening (0.556) is significantly higher than under the canopy (0.423) with F = 172.82, d.f. = 39, P <0.0001, $R^2 = 0.90$.

Table 5.2. Rate of decomposition (k), adjusted R^2, degree of freedom, F-values and P-values of curve-fitting procedure for possum dropping decomposition.

Location	k	Adj. R^2	d.f.	F	P
Open	0.556	0.947	19	337.744	<0.001
Canopy	0.423	0.893	19	159.380	<0.001

Significant difference in weight loss was not detected until 54 weeks after burial (Figure 5.14). Half life for litter in the open was 1.2 years (65 weeks) and for the under canopy litter was 1.6 years (85 weeks).

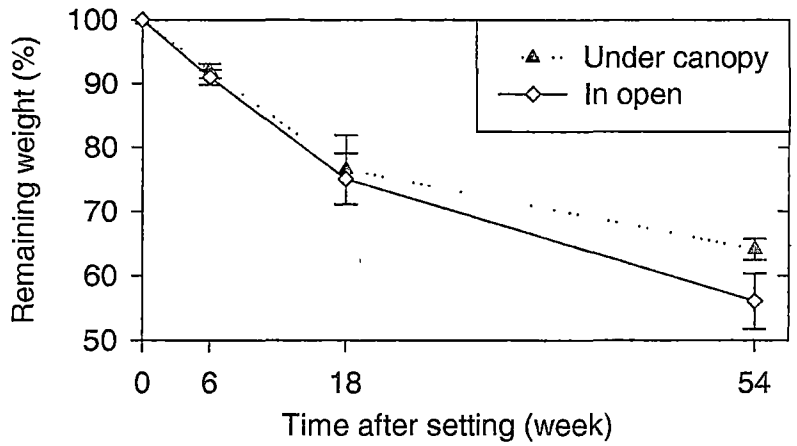

Figure 5.14. Comparison of possum dropping weight loss (% of initial weight) under the canopy and in the open.
Note: Vertical bars represent 95% confidence intervals.

5.3.4.3 Seasonal variations in *Eucalyptus globulus* leaf litter decomposition

In the first six weeks period of decomposition, there was a significant difference in the remaining weight of *Eucalyptus globulus* leaf litter incubated under the canopy in different seasons ($F = 4.14$, d.f. = 19, $P = 0.0237$). Decomposition of spring leaf litter (buried in August) is significantly lower (93.7% weight remaining) than decomposition of the leaf litter of any other seasons. The difference was more pronounced in the open than under the canopy ($F = 21$, d.f. = 18, $P < 0.0001$). Spring leaf litter in the open decomposed significantly slower with 92.9% weight remaining, and winter leaf litter (buried in May) decomposed significantly faster with only 82.4% weight remaining (Figure 5.15).

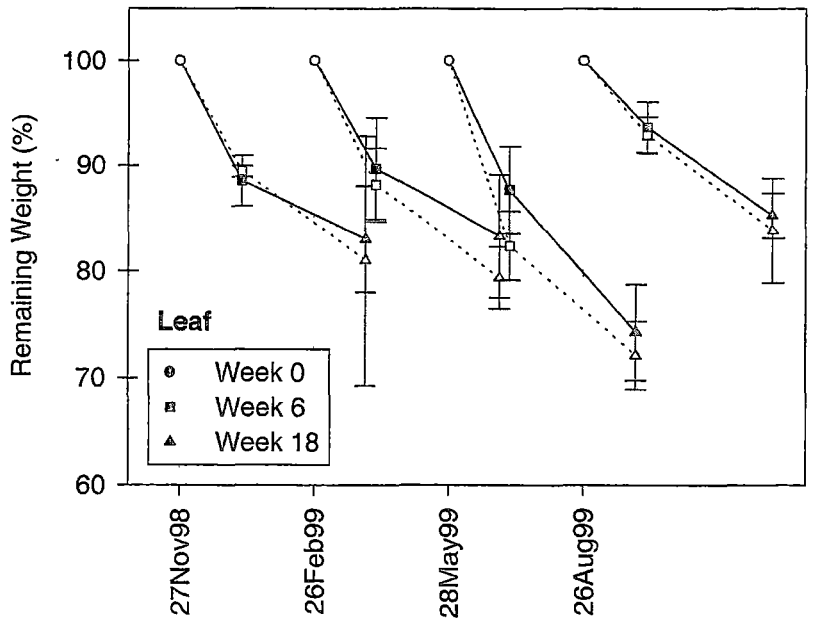

Figure 5.15. Comparison of the remaining weight of *Eucalyptus globulus* leaf litter buried at four different seasons.
Note: The shaded and open symbols represent under the canopy and in the open, respectively. Vertical bars represent 95% confidence interval.

A difference between spring (November), summer (February) and autumn (May) leaf litter was not apparent. Apart from the November litter, leaf litter under the canopy seemed to decay slower than leaf litter in the open, although the differences were not statistically significant.

Seasonal differences in *Eucalyptus globulus* leaf litter decomposition remain significant at week 18 ($F = 8.84$, d.f. = 19, $P = 0.0011$ for under the canopy; $F = 6.78$, d.f. = 18, $P = 0.0041$ for in the open). Autumn leaf litter continued to decay significantly faster than leaf litter from any other seasons (Figure 5.15). Decomposition of winter leaf litter was the slowest with 74.3% and 72.1% remaining weight under the canopy and in the open, respectively. These, however, were not statistically different to those from spring and summer leaf

litter. In any given season, leaf litter in the open decayed faster than the litter under the canopy although the differences were not statistically significant.

5.3.4.4 *Eucalyptus globulus* woody litter decomposition

The woody parts of *Eucalyptus globulus* litter decayed more or less at the same rate (Figure 5.16). There was not a significant difference between samples incubated under the canopy and in the open. The lack of statistical differences might be due to great data variability from samples in the open. Figure 5.16 shows that both branch and bark litter decayed faster in the open. In a year of decomposition they had lost five percent more than under the canopy. The difference, however, is not statistically significant.

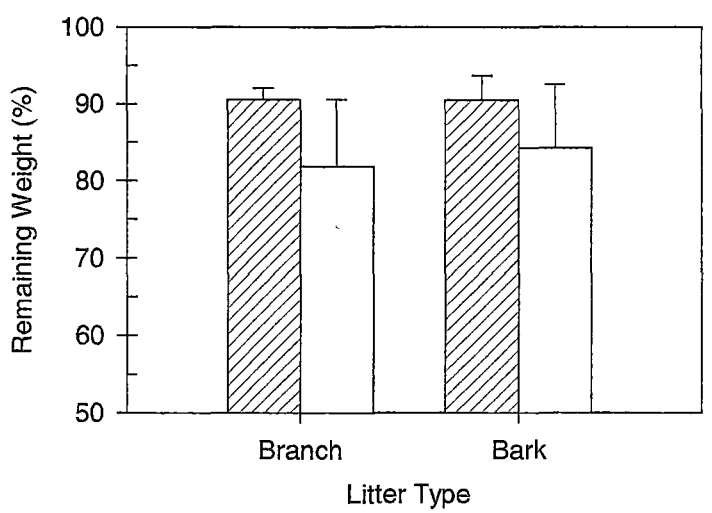

Figure 5.16. Comparison of the remaining weight of *Eucalyptus globulus* woody litter after one year decomposition under the canopy (shaded) and in the open (unshaded).
Note: Vertical bars represent confidence interval 95%.

5.3.4.5 Seasonal Variations in Possum Dropping Decomposition

At six weeks possum droppings under the canopy showed highly significant seasonal differences in decomposition ($F = 11.4$, d.f. = 19, $P = 0.0003$). The difference is more pronounced in the open ($F = 34$, d.f. = 19, $P < 0.0001$). At the sixth week of field incubation, spring (November) possum droppings under the canopy decayed at the slowest rate with 94.8% weight remaining. This figure is significantly different to that from summer (89.7% weight remaining) and autumn (86.0%).

The decay of possum droppings incubated in the open showed significance seasonal differences with a greater magnitude than decay under the canopy (Figure 5.17). Spring droppings decomposed slowest with 92.7% weight

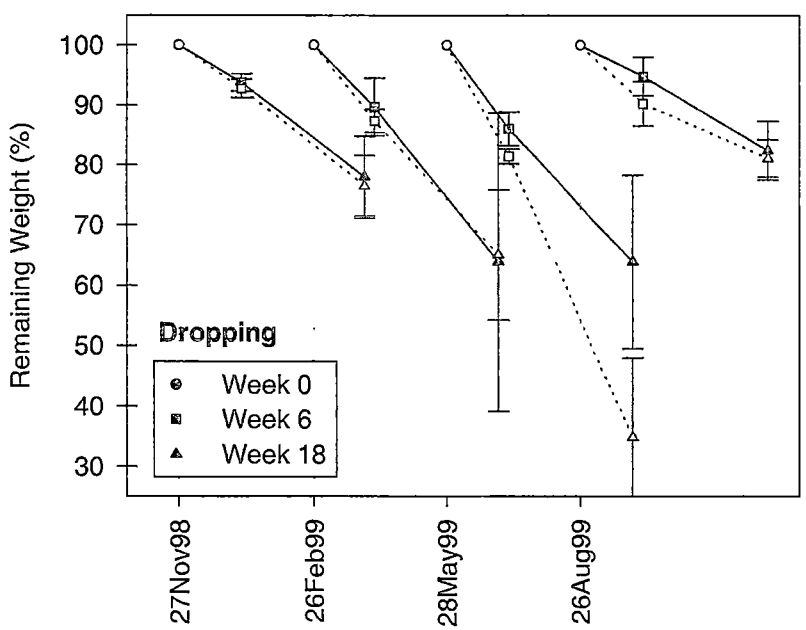

Figure 5.17. Comparison of the remaining weight of possum droppings after one year of decomposition under the canopy (solid lines) and in the open (dashed lines).
Note: Vertical bars represent confidence interval 95%.

remaining. The greatest weight loss occurred with autumn droppings, with only 81.4% of weight remaining.

The seasonal difference in possum dropping decomposition under the canopy became insignificant at week 18 mainly because of great data variability from summer (Feb) and autumn (May) samples (Figure 5.17). Yet, from Figure 5.17 it seems that they decayed faster than droppings from the other two seasons. Possum dropping in the open, on the other hand, shows a highly significant differences in decomposition ($F=41.3$, d.f. = 19, $P < 0.0001$). Autumn droppings decayed at markedly faster rate than droppings from any other seasons. The remaining weight dropped sharply to 35% of the initial setting during eighteen weeks of decomposition. The physical structure of the dropping had disappeared. It was effectively totally decomposed. The winter dropping decayed at a rate significantly slower than any other seasons, with 81.1% of the weight remaining.

5.3.5 Changes in Litter Nutrients

5.3.5.1 *Eucalyptus globulus*

Nitrogen contents of *Eucalyptus globulus* leaf litter showed a significant seasonal variation ($F = 5.88$, d.f. = 19, $P = 0.0066$). Autumn litter (May) started with nitrogen content significantly higher than litter from any other seasons. Nitrogen content of spring (Nov) leaf litter seems to increase with time (Figure 5.18). The difference, however, is not significant. Summer (Feb)

leaf litter nitrogen was affected by the canopy. There is a significant increase in nitrogen content in leaf litter in the open ($F = 17.6$, d.f. = 14, $P = 0.0003$) while the increase under the canopy is not significant. Nitrogen content of autumn (May) leaf litter declined in the first six weeks of decomposition and increased at week 18. The changes were more pronounced for litter under the canopy although they were not statistically significant. Winter (August) leaf litter nitrogen content did not significantly change during decomposition under the canopy. The change is significant in the open ($F = 4.26$, d.f. = 14, $P = 0.0400$).

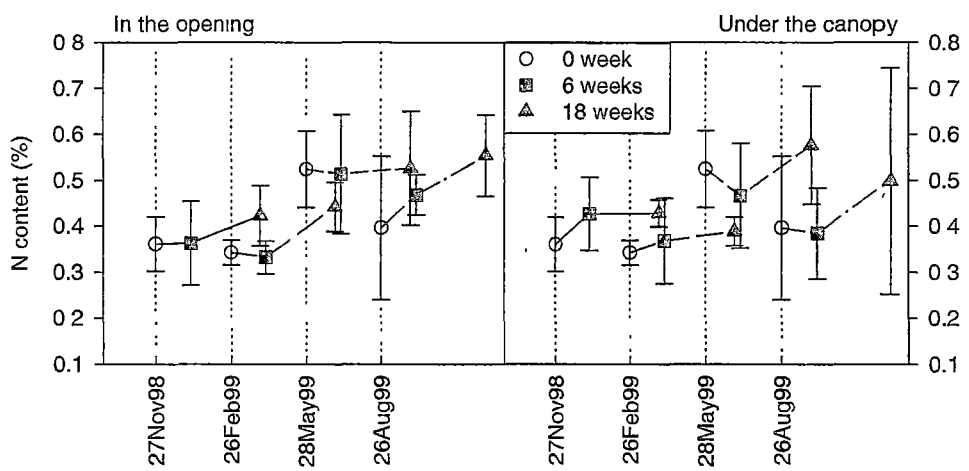

Figure 5.18. Changes in nitrogen contents of decomposing *Eucalyptus globulus* leaves.
Note: Vertical bars represent 95% confidence intervals. Materials from the same season started with the same concentration.

The initial phosphorus content of autumn (May) leaf litter was significantly higher than litter from any other seasons ($F = 44.4$, d.f. = 19, $P < 0.0001$). Phosphorus content of spring leaf litter changed significantly with time in open ($F = 8.83$, d.f. = 17, $P = 0.0015$) as well as under the canopy (Table 5.3).

Table 5.3. Changes in phosphorus content (ppm) during the decomposition of spring (Nov) litter of *Eucalyptus globulus* leaves under the canopy and in open.

Week	Canopy		Open	
0	155.6	b	155.6	b
6	169.6	b	149.9	b
18	192.0	ab	248.0	a
54	244.5	a	258.2	a

Note: Means followed by the same letter are not statistically different.

There is a small increase in phosphorus content of decomposing summer (Feb) leaf litter, but the change is not statistically significant, both under the canopy and in the open (Figure 5.19). Starting with a very high initial phosphorus content, autumn leaf litter reduced in phosphorus concentration as decomposition progressed (Figure 5.8). The changes were highly significant both under the canopy ($F = 16.4$, d.f. = 14, $P = 0.0004$) and in the open ($F = 12.4$, d.f. = 14, $P = 0.0012$).

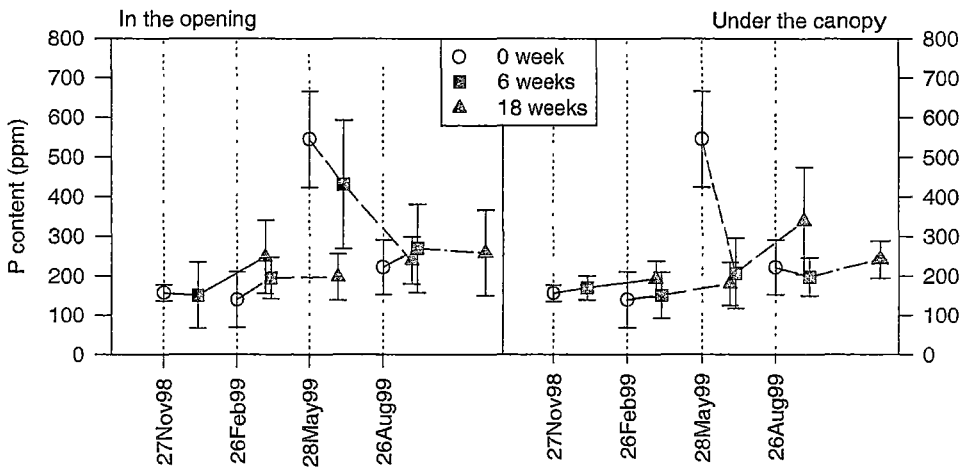

Figure 5.19. Change in phosphorus contents of decomposing *Eucalyptus globulus* leaves.
Note: Vertical bars represent 95% confidence intervals. Materials from the same season started with the same concentration.

In general, nitrogen contents in *Eucalyptus globulus* litter increased after one year of decomposition (Figure 5.20). As mentioned previously, there was a significant change in leaf litter nitrogen content. Nevertheless, the difference between under the canopy and in the open is not significant (Figure 5.20). Change in nitrogen content in bark litter was significantly more pronounced in the open than under the canopy ($F = 23.7$, d.f. = 14, $P < 0.0001$). There is a slight increase in bark litter nitrogen content but it is not statistically significant (Figure 5.20). Change in branch litter nitrogen is greater under the canopy then in open. The difference, however, is not statistically significant.

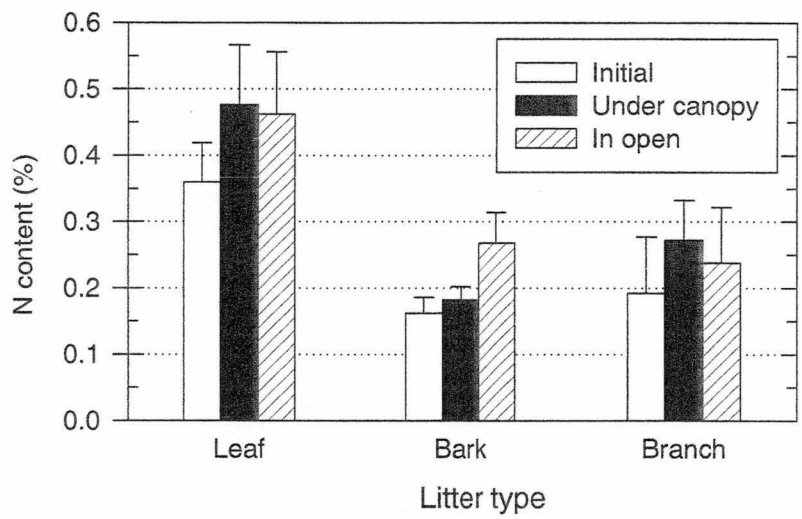

Figure 5.20. Change in *Eucalyptus globulus* litter nitrogen contents under canopy and in open after one year decomposition.
Note: Vertical bars represent 95% confidence intervals.

Phosphorus content in *Eucalyptus globulus* litter also increased with decomposition (Figure 5.21). Though there is a significant change in leaf litter phosphorus, the difference is not significant between under the canopy and in the open. The changes in phosphorus content in bark litter were highly significant ($F = 31.9$, d.f. = 14, $P < 0.0001$). In one year of decomposition, the

phosphorus content in the bark litter buried in open had increased fourfold. Bark litter under the canopy also increased in phosphorus content but the change was not statistically significant (Figure 5.21). Phosphorus content in branch litter also changed with time of decomposition. The magnitude of the change is greater in litter from the open. Though the increase in open litter is 61% of the initial concentration, the difference is not statistically significant.

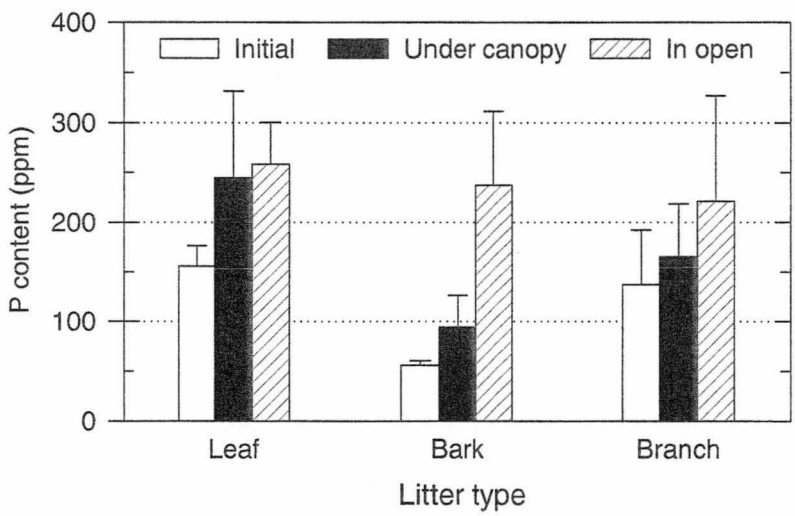

Figure 5.21. Change in *Eucalyptus globulus* litter phosphorus contents under canopy and in open after one year decomposition.
Note: Vertical bars represent 95% confidence intervals.

5.3.5.2 Possum Droppings

The initial nitrogen contents of possum dropping from various seasons were not significantly different ($F = 1.49$, d.f. = 19, $P = 0.2553$). There was a significant increase in nitrogen concentrations for spring (Nov) possum droppings incubated in the open space ($F = 4.22$, d.f. = 24, $P = 0.0122$; Figure

5.22). Afterwards, the increase was not significant. The increase of phosphorus in decaying dropping under the canopy was not statistically significant (F = 2.13, d.f. = 24, P = 0.1153).

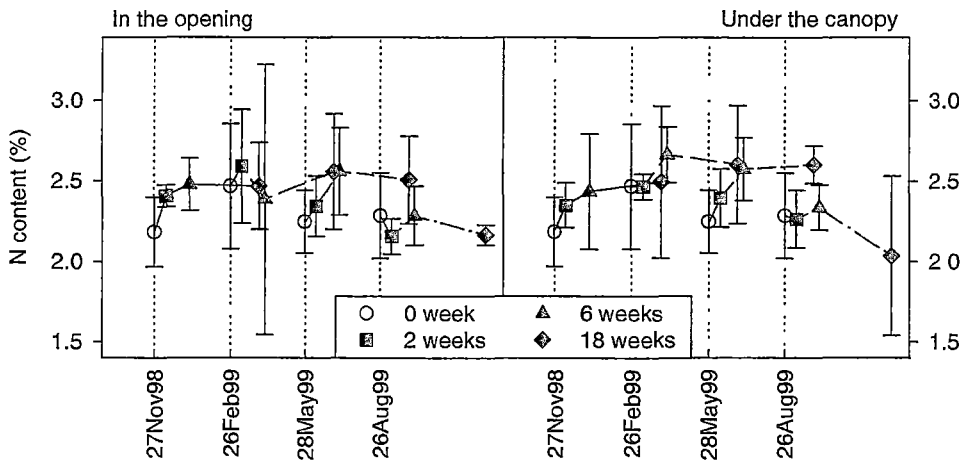

Figure 5.22. Nitrogen contents of decomposing possum litter in four different seasons.
Note: Vertical bars represent 95% confidence intervals.

Although there is an overall increase in nitrogen concentration during the decomposition of summer (Feb) droppings, the changes both in open and under the canopy were not significant (Figure 5.22). Autumn (May) dropping exhibited a significant change in nitrogen concentration during decomposition under the canopy (F = 6.83, d.f. = 19, P = 0.0036) but not in the open (F = 2.67, d.f. = 19, P = 0.0825) although the magnitude of the change was about the same. Nitrogen concentration in winter (Aug) droppings seemed to decrease during decomposition but the change was not statistically significant.

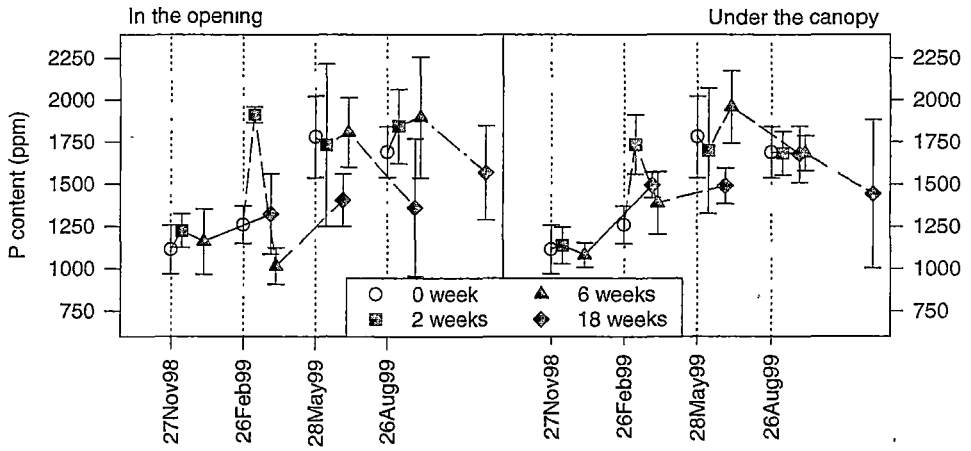

Figure 5.23. Phosphorus contents of decomposing possum litter in four different seasons.
Note: Vertical bars represent 95% confidence intervals.

The initial phosphorus contents of possum droppings in spring (Nov) and summer (Feb) were lower than in autumn (May) and winter (Aug) ($F = 28.2$, d.f. = 19, $P < 0.0001$; Figure 5.23). Changes in phosphorus content were evident in the decomposition of spring droppings. Phosphorus content at 18 weeks of decomposition in the open was significantly higher than any of the previous weeks ($F = 3.72$, d.f. = 24, $P = 0.0202$). Change in phosphorus content under the canopy was more pronounced ($F = 19.4$, d.f. = 24, $P < 0.0001$). The concentration markedly increased from the initial 1112.8 ppm to 1496.3 ppm. Autumn (Feb) phosphorus concentration showed a strange pattern with time. Figure 5.23 shows a very sharp increase in the second week of decomposition followed by a sharp drop at the sixth week then an increase at 18 weeks. Both change in the open and under the canopy were highly significant ($F = 87.9$, d.f. = 19, $P < 0.0001$ and $F = 14.1$, d.f. = 19, $P < 0.0001$, respectively) but the change was more striking in the open. Figure 5.23 shows that autumn (May) droppings declined sharply from 1806 ppm at the 6^{th} week

to 1361 ppm at the 18th week of decomposition in the open. However, the difference is not significant ($F = 2.67$, d.f. = 19, $P = 0.0825$). Changes under the canopy were not significant. Decomposition of winter (Aug) droppings did not show a significant change in phosphorus concentration, although Figure 5.23 shows a different pattern of changes under the canopy and in open.

5.4 Discussion

Phosphorus and nitrogen are evenly distributed around the tree and between the subcanopy and the open (Chapter 4). The expectation that stemflow would cause concentrated water flow near the trunk and therefore cause depletion of nutrients on the down side of the tree in a sloping soil was not realized in this study. Soil nutrient status in the soil is generally low, which may be caused by slow rate of decomposition and the poor nutrient status of litter as well as the inherited nature of the parent material. Based on the figures given in Chapter 4, the nitrogen pool in the 30-cm soil surface with a bulk density of 1.3 was equivalent to 9360 kg/ha, which is within the range of *Eucalyptus obliqua* open forests (4000-12000 kg/ha) but much lower than *Eucalyptus regnans* tall open-forest (17300 kg/ha) as summarized by Keith (1977). A phosphorus content equivalent to 19.58 kg/ha is much lower than the 8400 kg/ha in *Eucalyptus regnans* tall open-forests or the 731 kg/ha of *Eucalyptus marginata* open-forests (Keith, 1977).

Having found that nutrient concentration under the canopy and in the opening is not significantly different, the presence of *Eucalyptus globulus* does not seem to influence nutrient distribution in the soil. Since the sampling trees were richly surrounded by grassy vegetation, soil nutrient status in the open must have also been influenced by the grassy vegetation.

Seasonal variations in litterfall biomass, nutrient concentration and rate of decay are important to draw a complete picture of the nutrient budget in woodlands. For example, most of the *Eucalyptus globulus* leaf litterfall occurs in late summer (Figure 5.1), but at the same time the nitrogen concentration is about the lowest (Figure 5.7) and the decay rate is moderate (Figure 5.17). In contrast, the autumn leaf litterfall is very low, with nitrogen content at moderate levels, but the rate of decay is the fastest. The winter leaf litterfall is low but has a relatively high nitrogen content and the slowest decomposition rate. The same pattern is found in the seasonal variability of phosphorus except for the exceptionally high content in January litter. Nevertheless, the strongest determinant of actual contribution to the nutrient pool in the litterfall is the amount of litterfall rather than seasonal fluctuations in nutrient content.

The seasonal fluctuations in litter biomass, rather than variability in nutrient concentrations, determined the seasonal pools of nutrients in woody litter and animal droppings. The high phosphorus contents in possum droppings in June might relate to the production of new leaves following the large amount of leaf litterfall earlier on in March.

Most of the litterfall occurred under the canopy. If the same amount of litterfall occurred in the open, the release of nutrients from the litter into the system might became much greater, since the rates of decomposition of all types of litter were lower under the canopy. These slow rates might relate to restricted soil moisture content under the canopy. For example, only about ten percent of the precipitation equivalent to the area of the tree trunk (basal area) goes to the soil by throughfall (Figure 5.12). Water consumption by the tree may also reduce soil water content under the canopy. Reduced soil moisture under the canopy would restrict the microbial activity responsible for the early stage of *Eucalyptus globulus* leaf decomposition (Pareira *et al.*, 1998).

An increase in nutrient content during the first stage of decomposition is common (Hale and Pastor, 1998). Briones and Ineson (1996), observing the decomposition of *Eucalyptus globulus* leaves, attributed the loss to the release of ammonium, which peaked at the first seven weeks of decomposition followed by a steady decrease. They also found the total nitrogen and phosphorus contents in the leaf litter were higher at the end of their 13-week experiment. The overall leaf nutrient contents in their experiment (1.3% N and 0.06% P) were higher than those found at Conningham.

Pareira *et al.* (1998) also found an increase in nitrogen content of *Eucalyptus globulus* leaf litter in the first 11.5 months of decomposition, followed by a decline afterwards to a point even lower than the initial concentration. They related the increase in nitrogen content in the early stage of decomposition to litter materials that were low in nitrogen.

The inverse nitrogen concentration patterns in leaf litter (Figure 5.7) and woody litter (Figure 5.9) might confirm the mobilization of nutrients to stems or more permanent tree organs during senescence (Parrotta, 1999), which happens in late summer toward autumn. It might be a natural adaptation to seasonal climatic variation that leaves, buds and fruit litter were more common litter components during the summer through autumn period and that bark dominated the litter during the cooler seasons.

The decay rates of *Eucalyptus globulus* leaves (0.2943 under the canopy or 0.4144 in the open) are slower than the 0.808 in a mixed forest in Portugal (Pareira *et al.*, 1998). They are comparable to those of *Acacia longifolia* (0.468) and *Populus nigra* (0.393) in the same study. Nevertheless, the difference in decay rates of *Eucalyptus globulus* leaves under the canopy and in the open may cause a significant impact in the nutrient cycling especially in the first year budget.

Figure 5.24 shows the major pool of nutrients in litter materials related to *Eucalyptus globulus*. Data availability restricts the presentation to litterfall under the canopy. The proportional contribution of the litter component was based on a one year flux to the soil under the canopy. The majority of nutrients originated from the leaf litter, although most of litter biomass comes from bark. Bud litter is an important phosphorus pool. Though it comprises only about 10% of total litter standing biomass, phosphorus contribution from buds exceeds that of bark at above 20% of total phosphorus pool in the total litterfall.

Studies in throughfall and stemflow usually relate to interception of rainfall by the canopy (e.g. Smith, 1974). In the present study, throughfall and stemflow are presented in terms relative to both the size of the tree and the amount of rainfall (Westman, 1978). The results have shown that the amount of stemflow in *Eucalyptus globulus* trees grown in an open woodland in Conningham can be concentrated up to six to eleven times higher than the amount of rain falling on the area of the trunk. This maximum exaggeration happens in the mid-sized trees. The higher relative stemflow in the mid-sized trees was probably caused by exposure of bare trunk to the rain that came in side-way directions. Plenty of young leaves in small trees might prevent this happening and the massive canopy of big trees may also prevent the rain directly hitting the trunk. This may explain why there are low relative stemflow in the small and big trees. In this regard, stemflow could become an important mechanism that brings about changes in the physical nature of the soil near the trunk.

Although it was thought that stemflow could be an important agent of nutrient cycling, the nutritional contribution of stemflow was very low in the present study (Figure 5.24). Ranging from 0.20 -1.49 ppm, total nitrogen concentration in stemflow is very low compared to the 3.6 ppm reported by Westman (1978). Phosphorus content is very low, as also reported in Westman's study (<0.01ppm). The amount of throughfall was much lower than stemflow, with even lower nutrient concentrations. Consequently, the amount of nutrients reaching the soil by throughfall was also very low.

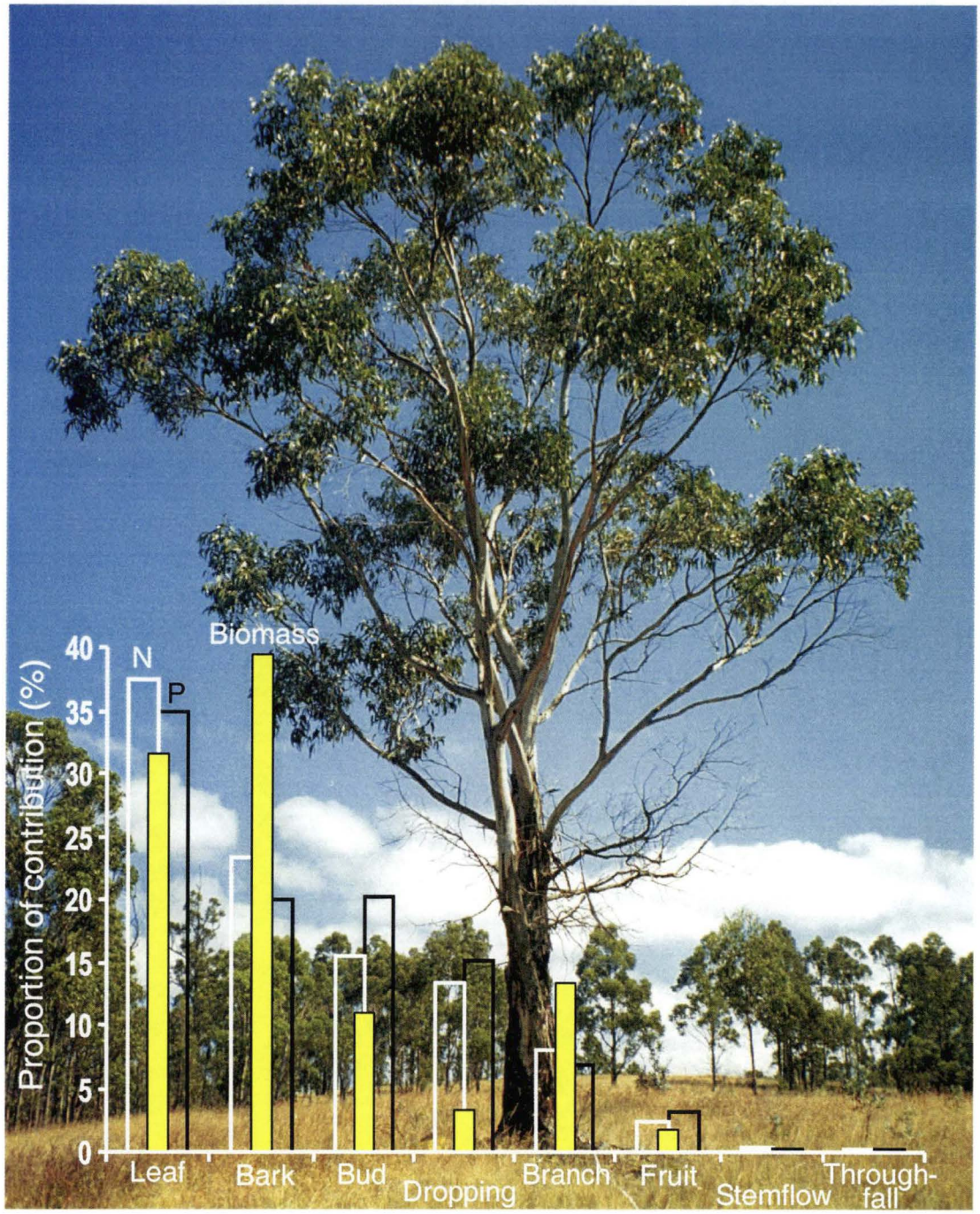

Figure 5.24. Proportion (%) of standing biomass and nutrient pools of various *Eucalyptus globulus* litter components, possum droppings, stemflow and throughfall.
Note: There is no standing biomass for stemflow and throughfall.

Figure 5.25 and 5.26 summarize the dynamic of nutrient pool in the various litter types and, based on the exponential decay rates and nutrient concentration found in this study. The release of nutrients under the canopy and in the open is presented.

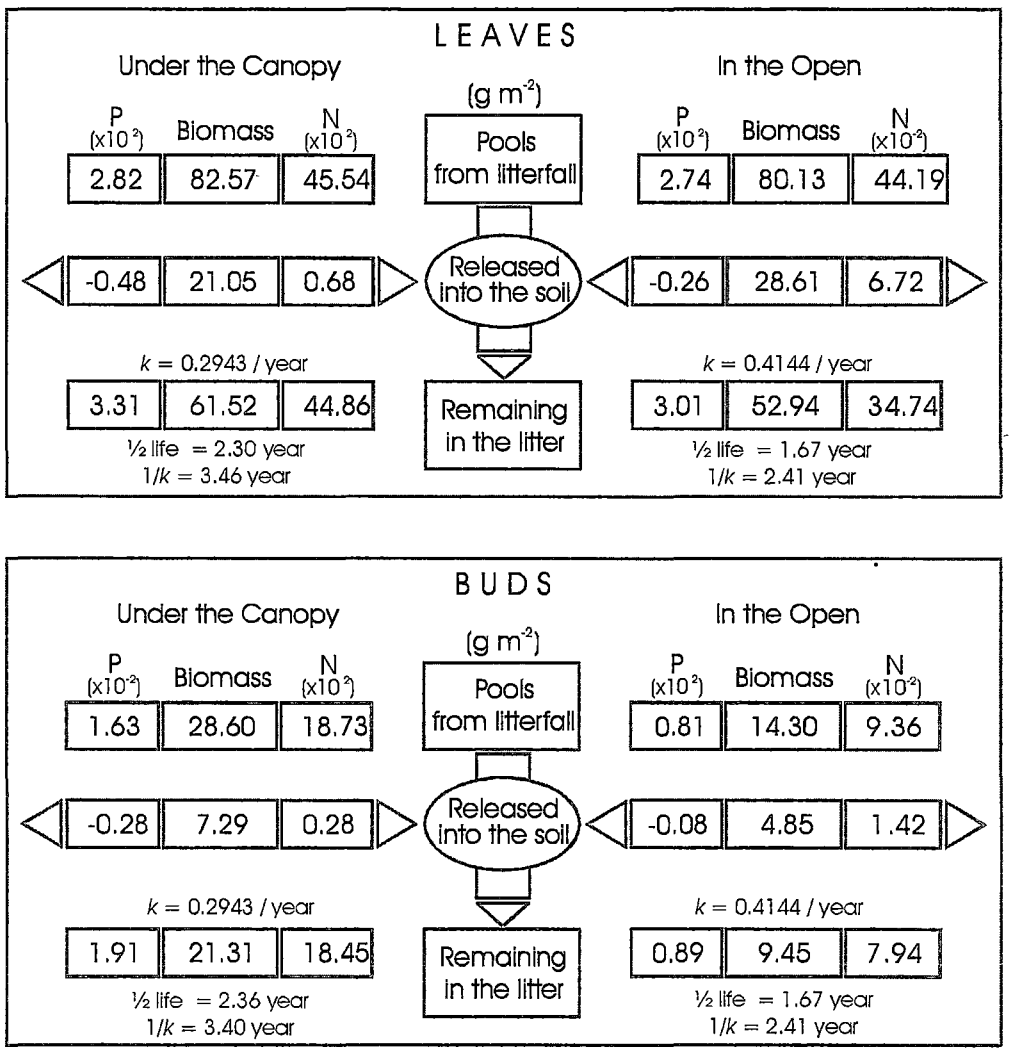

Figure 5.25. Flows of nutrients from *Eucalyptus globulus* litter during one year decomposition including half life and residence time (1/*k*).

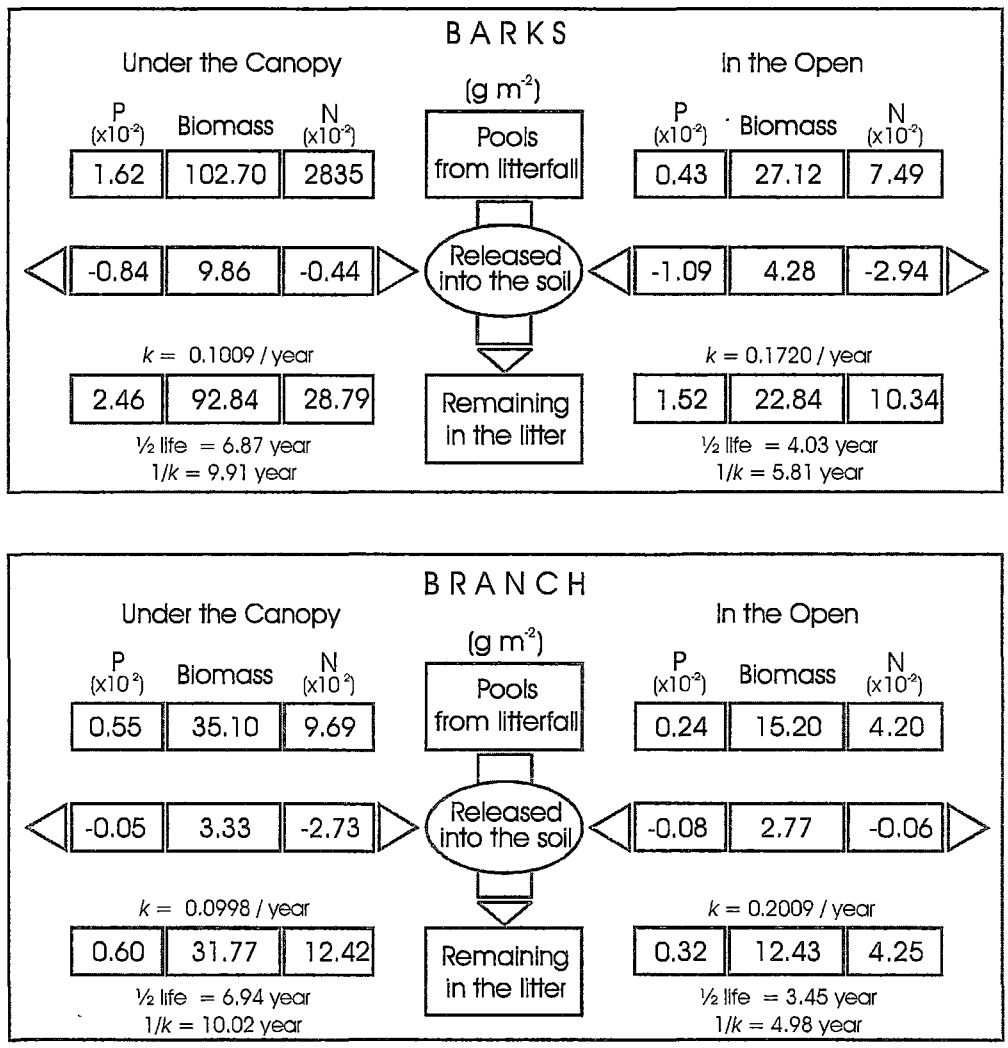

Figure 5.25. (continued)

The decay rates and hence the mass loss exhibited the difference between under the canopy and in the open. The relative bareness under the canopy may have caused a greater exposure to sunlight and accelerated the drying of the litter, while litter in the open was well protected by the grassy vegetation. The entrapment of large portion of precipitation by the canopy (Figure 5.12) may also reduce water availability under the canopy. The large amount of water supply through the stemflow (Figure 5.11) may have been too concentrated to

provide evenly distributed moist conditions in the soil under the canopy. Considering the involvement of micro-organisms and arthropods (Pereira *et al.*, 1998) and chemical processes (Briones and Ineson, 1996) during decomposition, water restriction may be the primary caused of the low decay rates under the canopy. The reduction of decay rates under the canopy of *Eucalyptus globulus* affected not only all litter originated from the plant but also animal droppings, which have decay rates that are much higher than other litter components.

There was 6.72 x 10^{-2} g/m^2 annual release of nitrogen to the soil in the open from leaf litter. This is much higher than the release from bud litter (1.42 x 10^{-2} g/m^2) or possum dropping (0.47 x 10^{-2} g/m^2; Figure 5.26). The budget under the canopy, however, is different. The majority of nitrogen released from the litter comes from possum droppings (3.52 x 10^{-2} g/m^2) compared to only 0.68 x 10^{-2} g/m^2 from the leaf litter and 0.28 x 10^{-2} g/m^2 from bud litter.

Wildlife may be an important component in the cycle of nutrients in the *Eucalyptus globulus* dominated woodlands. In addition to the rapid decay of possum dropping, the average monthly range of nutrient contents in possum droppings (1.5-2.29 % N and 1124-2248 ppm P) were remarkably higher, compared to other litter materials. The average monthly ranges for *Eucalyptus globulus* litter were 0.43-0.76 % N and 264-457 ppm P for leaves, 0.46%-1% N and 608-747 ppm P for buds, and 0.17-0.39 % N and 89-263 ppm P for bark. Nevertheless, judging from the amount of droppings collected in the litter trap (less than 1 g/m^2), the number of possums at Conningham must have

been low, or, perhaps, the solitary trees were less preferred by the animals. It must be noted that *Eucalyptus globulus* is an important diet for possum all year long, as traps under the canopy constantly collected more dropping than in the open, and a seasonal pattern of dropping litterfall could not be clearly identified.

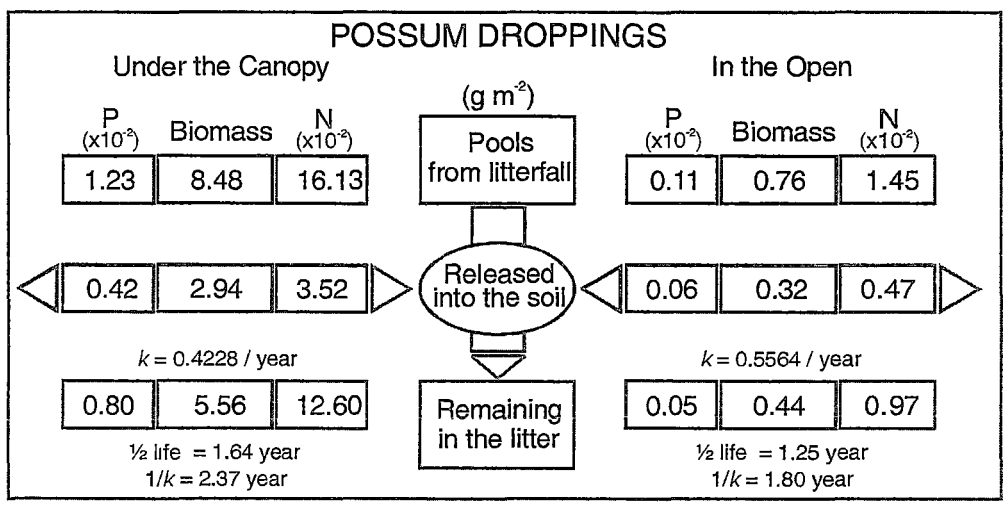

Figure 5.26. Flow of nutrients from possum droppings during one year decomposition including half life and residence time (1/*k*).

The decay rate of *Eucalyptus globulus* leaf litter in this study was comparable to that of other species. O'Connell (1997) revealed that the half life of the resistant components of *Eucalyptus diversicolor* leaves was 2.27 years (118 weeks). The labile components of the leaf litter decayed half of their weight within three weeks. On average, the half life of *Eucalyptus globulus* leaf litter at Conningham is 2.30 years (120 weeks) under the canopy and 1.67 years in the open.

The average half-life of the wood litter reported in O'Connell's (1997) study is 5.77-7.40 years (300-385 weeks). In the present study, it averages 4.03 and 6.87 years for bark litter in the open and under the canopy, respectively, and in the same manner 3.45 and 6.94 years for branch litter.

Total nutrient content in the bark is large (Figure 5.25). However, bark litter may not contribute proportionately to nutrient cycling. In the early stage of decomposition it may immobilize nutrients from the surroundings, showed by the negative signs in the "release box" in Figure 5.25. This indicates that, in the first year of decomposition, the release of nutrients in the biomass loss of woody litter did not compensate for the withdrawal of nutrients from its surroundings, most likely as a result of microbial activity (Austin and Vitousek, 2000). However, the presence of bark may influence microclimate and organic matter balance under the canopy. Dried bark and branches are also a major component of fuel for fires.

The seasonal nature of litterfall pertains not only to the amount of litterfall, but also to the nutrient concentration in the litter. This, in turn, has a great impact on seasonal nutrient distribution. Bark makes the greatest contribution to total standing biomass of litterfall, followed by leaves, branch, buds and fruits. Possum droppings constitute only a small fraction.

With regard to the storage capacity of nutrients, however, leaves are the major pool of nitrogen, followed by bark. The nitrogen pool in both buds and possum droppings exceed that in branches. Bud litter is even more important

than the bark in the phosphorus pool. The overall order of importance in the nitrogen pool is leaf, bark, bud, possum dropping, branches, fruit, stemflow and throughfall. The order for phosphorus is leaf, bud, bark, droppings, branches, fruits, stemflow and throughfall.

Although the actual amount of possum dropping is small, the flux of nutrient (both nitrogen and phosphorus) under the canopy is mainly supplied by possum droppings, as a result of a remarkably high decomposition rate. During the first year of decomposition, possum droppings are the only litter component that release phosphorus to the system. Decay rates can be explained satisfactorily with the negative exponential decay model.

CHAPTER 6

General Conclusions

The research hypotheses of this thesis are that: (1) *Eucalyptus globulus* creates environmental heterogeneity; (2) this induced environmental heterogeneity is reflected in the species richness of the woodland.

It has been demonstrated that *E. globulus* creates environmental heterogeneity in life, and after death. In life, trees of *E. globulus* influence the input of moisture to the soil through stem flow and throughfall, resulting in a much lesser accession of moisture to the soil than outside their canopies (Chapter 5). The litter, and nutrients in litter, below their canopies is much greater than outside their canopies, yet soil nutrients do not differ, because of the effects of dryness on decomposition rates (Chapter 5). The trees trap sediments above their trunks and their roots bring rocks to the surface (Chapter 4). A relatively bare zone is created around the trunk (Chapter 4).

In death, the nature of the influences is more unusual. The presence of fallen trees may intensify the damaging impacts of fire on soils. Long-lasting, linear bare patches within the otherwise well covered understorey of grassy open-forest in Conningham State Recreational Park mark the past locations of the trunks of fallen trees. Comparisons of the physical, chemical and biological properties of the soil were made between these log shadows and the neighbouring, vegetated ground. The bare ground of the log shadows has a coarse soil texture that permits fast water movement through the soil. This soil texture is consistent with the known effects of high temperatures on soils. Low rainfall combined with poor water holding capacity may account for the prolonged relative bareness of the log shadows, given that nutrient differences and

differences in microbial antagonism are not consistent with their patterning (Chapter 2).

There is a strong, but not conclusive, case that the presence of *E. globulus* trees increases the species richness of the woodland. In both the cases of the log shadows (Chapter 3), and the bare zones around the bases of trees (Chapter 4), species composition was different from the adjacent fully-vegetated areas. There are four distinct groups of taxa: (1) those with a bare ground preference (e.g. *Ozothamnus purpurescens*, *Agrostis*, *Bursaria spinosa*, *Danthonia*, *Dichelachne*, *Euchiton*); (2) those that avoided bare ground (e.g. *Hypericum gramineum*, *Dianella revoluta*, *Carex breviculmis*, *Dichondra repens*, *Senecio*, *Trifolium*); (3) those more abundant outside bare ground that penetrated it nevertheless (*Poa*); (4) those that were indifferent. Without the bare ground created by trees, the group 1 species would have much less bare ground in which to establish. However, only a few of these species were not found in fully vegetated areas. It is therefore safer to conclude that the presence of *E. globulus* trees influences local patterns of species distribution, rather than site species richness, although at the quadrat scale there is no doubt that species richness would be lower in the absence of the trees.

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